OPTIMAL MANAGEMENT OF BIOLOGICAL POPULATIONS

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OPTIMAL MANAGEMENT OF BIOLOGICAL POPULATIONS

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The successful management of biological populations is essential to both the world's economic and environmental wellbeing. This includes controlling invasive species and sustainably harvesting biological resources for profit.

In the first chapter we consider monitoring programs for the management of invasive populations that we wish to eradicate. Previous theoretical studies have argued that managers are allocating too much effort to programs for determining the location of invasive species in a managed area. In contrast, managers view early detection as the key to invasive species management. Intuitively, the importance of early detection makes sense because early detection can lead to early intervention and therefore massive ecological and economic benefits. In this chapter we provide a theoretical explanation for why it is optimal to deploy an intense initial search for the invader and why past studies have underestimated optimal surveillance effort.

In the second chapter we consider populations that are harvested for profit. Due to high economic and ecological stakes in determining sustainable harvest policies for renewable resources, such as timber, fish and game, optimal harvest is a widely studied problem in bioeconomics. However, most of the work focuses on simple models for the harvest of unstructured populations, even though demographically structured population models are more commonly used for population assessment. In this chapter we derive optimal escapement rules for both deterministic and stochastic stage-structured population models. When considering environmental stochasticity, optimal harvest of the pre-reproductive life stage is

either more aggressive or more conservative than in the deterministic case, depending on the second and third derivative of the recruitment function. However, when harvesting reproductive adults, optimal harvest is the same as in the deterministic case.

In the third chapter we ask "how much do these optimal management plans, generated using simplified models, perform when a population is more complex?" Can a manager use their expert judgment and flexibility to outperform simple models that make incorrect assumptions about population dynamics? As a first step towards answering this question, we conducted experiments where human subjects managed a hypothetical simulated population, by playing an online game, and compared their performance to the performance of decisions developed by mathematical models. The models, *on average*, outperformed human judgment, even when they made incorrect assumptions about the simulated population's dynamics. However, in some scenarios the models produced undesirable results. Therefore, we recommend that managers use mathematical models as a supplement, rather than a replacement, for expert judgment.

BIOGRAPHICAL SKETCH

Matthew Holden was born in Santa Monica, California. He studied at the University of California, Davis, receiving a B.S. in Applied Mathematics with a minor in Ecology, Evolution and Biodiversity (2008). If all goes well, he will begin an appointment as a Postdoctoral Research Fellow in the Biodiversity and Conservation Science Centre at the University of Queensland, in Brisbane Australia.

In memory of my mother Jackie Holden

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

MATHEMATICAL BACKGROUND

In this thesis we use optimal control theory and dynamic programming arguments to solve problems in natural resource management, and therefore we start by briefly introducing the reader to these topics.

1.1 Dynamic programming

Consider a dynamic decision problem of the form

$$\min_{u_t \in \mathscr{U},\, t\in\{0,1,\ldots,T\}} \left\{ \sum_{t=0}^{T} F(x_t, u_t, t) \; + \; S(x_T, T) \right\}$$

$$\text{subject to} \tag{1.1}$$

$$x_{t+1} = f(x_t, u_t, t),$$

$$x_0 = \bar{x} \text{ given.}$$

That is, we have some biological resource or pest that we wish to manage over a length of time, T, whose state in the next time step, x_{t+1}, is a function of the current state, x_t, and in addition the management action we chose in time t, u_t. This time dependent *control*, u_t, takes on a value from a set of possible management actions, $\mathscr{U}$, which can be a continuous set (e.g. $\mathscr{U} = [0, 1]$, where u_t is the proportion of the resource we choose to remove from the system at time t) or finite (e.g. $\mathscr{U} = \{0, 1\}$, where u_t is one if we choose to spray pesticides and zero if we don't). The goal for the manager is to choose u_t at each time step such that

some objective function (the value of the bracketed term in (1.1)) is minimized (or maximized). The objective function is usually measured in economic costs or benefits but could also include terms that factor in ecological goals that do not have intrinsic monetary value. The scrap function (also called a "terminal cost function" or "exit penalty"), $S(x_T, T)$, represents the cost or benefit of leaving the system in state x_T at the end of the management period. For most of this thesis we set it equal to zero because we consider long management windows. However, for short term management problems, it should be included when there is large ecological or economic rewards for leaving the system in a desirable state after management.

When u and x can take on any value in a continuous subset of the real numbers, we can solve (1.1) by the method of Lagrange multipliers. Here, the difference equation in (1.1) is the constraint, and the problem can be solved by simple multivariable calculus. We use this method to solve for optimal harvest strategies in a stage structured fishery in Chapter 3. However, such methods do not work for finite sets of possible management actions and it is also difficult to extend this method to problems where the state dynamics are stochastic.

In these cases dynamic programming can be used to find a solution to (1.1). The method is based on *Richard Bellman's Principle of Optimality* (Bellman, 1952) which states:

> An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision.

This can be translated into the language of mathematics by using value functions.

Define

$$V(x_\tau, \tau) = \min_{u_t \in \mathscr{U},\, t \in \{\tau,\ldots,T\}} \left\{ \sum_{t=\tau}^{T} F(x_t, u_t, t) \,+\, S(x_T, T) \right\}, \tag{1.2}$$

the value of the system being in state x_τ in time τ. By Bellman's Principle of Optimality,

$$V(x_\tau, \tau) = \min_{u_\tau} \left\{ F(x_\tau, u_\tau, \tau) + V(\, x_{\tau+1},\, \tau + 1) \right\}. \tag{1.3}$$

From here, one can proceed iteratively, backwards in time, calculating the optimal management decision in time $\tau - 1$, given the optimal management decision in time τ, either by using a computer or in some special cases analytically (by recognizing a pattern). This is known as the method of dynamic programming.

Dynamic programming can easily be extended to stochastic problems where one wishes to maximize the expected value of the objective function, by exploiting the properties of the expectation operator. In Chapter 3, we use this method to solve for optimal harvest strategies for a stochastic stage structured fishery where we are able to exploit a pattern in the value function that allows us to solve the optimization problem analytically.

1.2 Pontryagin's minimum principle

In Chapter 2 of this thesis, we study the optimal management of invasive species framed as a continuous time decision problem, analogous to the discrete time problem in (1.1). That is,

$$\min_{u(t)\in\mathscr{U}} \left\{ \int_0^T F(x(t),u(t),t)\,dt \;+\; S(x(T),T) \right\}$$
$$\text{subject to} \qquad (1.4)$$
$$\frac{dx}{dt} = f(x(t),u(t),t),$$
$$x(0) = x_0 \text{ given.}$$

From here on out I will usually write $x(t)$ and $u(t)$ short hand as x and u, respectively, to make the equations less cumbersome. Note that in this case, unlike (1.1), the dynamics are governed by a differential equation, and the set of possible controls, $\mathscr{U}$, is a set of functions, not numbers. To solve (1.4), we use *Pontryagin's minimum principle*. A version of the minimum principle can be derived using a dynamic programing argument. Define the value function for the above problem,

$$V(x,t) = \min_u \left\{ \int_t^T F(x,u,\tau)\,d\tau \;+\; S(x(T),T) \right\}, \qquad (1.5)$$

To simplify our argument, we consider an unconstrained u, and assume $F(x,u,t)$ is not linear in u. By the Bellman principle of optimality, for some time interval Δt, this is just

$$V(x,t) = \min_u \left\{ \int_t^{t+\Delta t} F(x,u,\tau)\,d\tau \;+\; V[x(t+\Delta t),\, t+\Delta t] \right\}. \qquad (1.6)$$

If we assume V is smooth, then we can Taylor expand $V[x(t+\Delta t),\, t+\Delta t]$, divide through by Δt, cancel terms and take the limit as $\Delta t \to 0$, to obtain

$$\frac{\partial V(x,t)}{\partial t} = -\min_u \left\{ F(x,u,t) + \frac{\partial V(x,t)}{\partial x} f(x,u,t) \right\}, \qquad (1.7)$$

known as the *Hamilton-Jacobi-Bellman equation* (Bellman, 1954). This equation provides a necessary and sufficient condition for u to be optimal. However, in practice, solving this equation (almost always numerically) can be quite difficult and is still an active area of research. Instead, the Pontryagin minimum principle provides equations that form a necessary condition for u to be optimal, which are often easier to solve.

Denote u^* as the optimal control and x^* as the associated optimal state and define $\lambda(t) \equiv \partial V(x^*, t)/\partial x$, the amount a manager would be willing to pay for an infinitesimal change in the state variable, called the adjoint variable or shadow price. Also define

$$H(x, u, \lambda, t) \equiv F(x, u, t) + \lambda f(x, u, t), \tag{1.8}$$

called the Hamiltonian. Differentiating both sides of (1.7) by x we obtain

$$\frac{d\lambda}{dt} = -\frac{\partial H(x^*, u^*, \lambda, t)}{\partial x}. \tag{1.9}$$

With (1.9) and the fact that $\dot{x} = \partial H/\partial\lambda$, by the problem statement (1.4), we see why H is called the Hamiltonian. Equation (1.9) is the main component of the classic statement of Pontryagin Minimum Principle, which gives necessary conditions for a control $u(t)$ to be optimal. Note that the heuristic argument we gave above requires strong assumptions on the differentiability of V. This can be relaxed quite substantially to give the full statement of Pontryagin's minimum principle.

Theorem 1.1 (Pontryagin's Minimum Principle)**.** *If $u^*(t)$ is an optimal control for* (1.4) *and $x^*(t)$ is the associated state, then there exists a piecewise differentiable*

adjoint variable $\lambda(t)$ *such that*

$$H(u, x^*, \lambda, t) \geq H(u^*, x^*, \lambda, t) \tag{1.10}$$

for all controls u *at each time* t*, and*

$$\begin{aligned} \frac{d\lambda}{dt} &= -\frac{\partial H(x^*, u^*, \lambda, t)}{\partial x} \\ \lambda(T) &= \frac{\partial S(x^*(T), T)}{\partial x}. \end{aligned} \tag{1.11}$$

We used dynamic programing to explain the intuition behind this theorem. Alternatively, one can arrive at the minimum principle by using Lagrange multipliers. This involves converting (1.4) to the analogous discrete time problem by using a Riemann sum to approximate the objective function and a finite difference equation to approximate the differential equation governing the state dynamics. One then sets up the Lagrangian, takes the limit as the step size goes to zero, and then, rather cavalierly, proceeds to perform the method of Lagrange multipliers to derive the minimum principle above (pgs. 152-153 in Dixit, 1990).

1.3 Relation to the calculus of variations

Pontryagin's minimum principle can be thought of as an extension of the Euler-Lagrange equation, from the calculus of variations, to a more general class of problems. Minimizing the functional, $\int_a^b F(x(t), x'(t), t)\, dt$, is a special case of problem (1.4), where $x'(t) = u(t)$, $S(x, T) = 0$, and where $u(t)$ is unconstrained. In such a case, a necessary condition for $u^*(t)$ to be optimal is that $\partial H/\partial u = 0$ at $u(t) = u^*(t)$, for all t. Differentiating the Hamiltonian by u, solving for λ and then differentiating by t yields

$$\frac{d\lambda}{dt} = -\frac{d}{dt}\left[\frac{\partial F}{\partial u}\right], \tag{1.12}$$

Which we can combine with (1.11) to get the Euler-Lagrange equation

$$\frac{\partial F}{\partial x} - \frac{d}{dt}\left[\frac{\partial F}{\partial u}\right] = 0. \tag{1.13}$$

We chose to use dynamic programing to give a heuristic argument for the Pontryagin Minimum Principle, as we will use dynamic programming in Chapter 3 of this thesis. However, we could have used a calculus of variations argument to derive a version of Pontryagin's Minimum Principle. To do so, we would start by assuming $u^*(t)$ is optimal, define an ϵ perturbation $u_\epsilon(t) = u^*(t) + \epsilon\, h(t)$, and show that (1.8) and (1.11) imply the derivative of the objective functional evaluated at u_ϵ, with respect to ϵ, is zero at the point where $\epsilon = 0$, as outlined in (pgs. 7-12 in Lenhart and Workman, 2007).

1.4 Summary

In this chapter we gave an overview of the optimization methods we use to solve natural resource management problems by introducing the reader to the concepts of dynamic programming, Lagrange multipliers, the Hamilton-Jacobi-Bellman equation, Pontryagin's minimum principle and the calculus of variations. Note that we have sacrificed mathematical rigor in order to intuitively see the connections between all of these mathematical tools. For the full 33 page, rigorous, proof of the Pontryagin minimum principle see (Pontryagin, 1987)

CHAPTER 2

OPTIMAL SURVEILLANCE FOR INVASIVE SPECIES MANAGEMENT

Abstract

Government agencies develop invasive species management programs assuming that early detection is key to successful management. However, theoretical studies have suggested that managers are investing too heavily in sampling to detect new local invader populations. This is a paradox; how can early detection seem so important when theory suggests otherwise? Using optimal control theory to develop surveillance policies that minimize the total cost of sampling, eradication, and damage by the invasive, we find that the best strategies use intense early sampling, followed by reduced sampling effort. In contrast, past theoretical work has mostly been restricted to constant sampling effort strategies, potentially underplaying the importance of surveillance. Intense early sampling drastically reduces costs compared to the best constant effort strategies if propagule pressure from outside the managed area is low. However, when new infestations tend to result from independent introductions, instead of local spread that a manager can prevent through detection and eradication, intense early sampling provides minimal cost savings over the constant strategies calculated in the literature. Invasive species with low introduction rates, such as *Anoplophora glabripennis* (Asian longhorned beetle), warrant an initial period of intense surveillance. This is especially true if the invader spreads quickly, such as many invaders of fresh water lakes. However, for managers sampling to eradicate isolated *Lymantria dispar* (gypsy moth) populations on the west coast of the US, constant-effort sampling will be cost effective because of the high propagule pressure from established populations in the Northeast US.

2.1 Introduction

Invasive species cause hundreds of billions of dollars of damage to urban infrastructure, agriculture, livestock, fisheries, and natural ecosystems (Pimentel et al., 2005; Davis, 2009). There is a rich literature describing the optimal management of established invasive species under complete knowledge of population abundance (see Epanchin-Niell and Hastings (2010) for a review). However, only recently has the focus of optimal invasive species management shifted towards the design of surveillance programs for invasive species whose distribution is uncertain (Mehta et al., 2007; Bogich et al., 2008; Hauser and McCarthy, 2009; Haight and Polasky, 2010; Homans and Horie, 2011; Epanchin-Niell et al., 2012; Horie et al., 2013; Epanchin-Niell et al., 2014; Rout et al., 2014).

These theoretical optimal monitoring programs clash with management intuition. Biologists and managers widely recognize that intense monitoring and early detection are key components of successful invasive species management (Hobbs and Humphries, 1995). In fact, "early detection and rapid response" is one of five main sections of the United States' official *National Invasive Species Management Plan* (National Invasive Species Council, 2008). However, when theoretical optimal monitoring strategies have been compared to what managers actually do in the field, nearly all suggest that managers are sampling too much (Bogich et al., 2008; Epanchin-Niell et al., 2012). For example, using data on Gypsy Moth in Washington, Bogich et al. (2008) found that managers were deploying traps at densities approximately 20 times greater than the "optimal" solution. Is nearly 95 percent of the sampling deployed in Washington really a waste of money? And if so, how general are these results?

Due to model and methodological simplifications, previous theoretical stud-

ies have largely explored surveillance strategies that are static in time by either (1) calculating the most cost effective time constant sampling strategy (Mehta et al., 2007; Bogich et al., 2008; Epanchin-Niell et al., 2014), (2) solving for optimal sampling effort assuming the pest is at an economic equilibrium density (Epanchin-Niell et al., 2012), or (3) focusing on surveillance at a single moment in time (Hauser and McCarthy, 2009; Horie et al., 2013; Rout et al., 2014). However, because early detection can lead to early intervention, we might expect optimal sampling effort to be more intense early during a management program. If this is the case, theory could be vastly underestimating optimal sampling effort.

In this paper we generate rules of thumb for when intense initial sampling, followed by a sharp decrease in sampling effort, is more cost effective than strategies that are constant through time. For invaders with high rates of establishment from an outside source, the constant strategies in the literature are likely cost effective and managers may be sampling too much. However, if the invader spreads much faster than the rate at which it is being introduced from an outside source, constant sampling strategies underestimate optimal sampling effort early during the management program. When the local spread of the invasive is fast and propagule pressure is low, intense efforts for early detection are, in fact, key to cost effective management.

When classifying invasions into the categories of high and low introduction rates, it is important to consider the spatial scale of management. At a national scale, long distance or human mediated dispersal may be considered local spread, while for a farm, park or city such dispersal may be part of the introduction rate. Therefore, even if constant strategies are cost effective for managing a pest in one situation, a manager controlling the same species in another situation may need

to increase sampling early in order to minimize total costs.

2.2 Methods

2.2.1 Ecological model

Resolving the strong disagreement between mathematical results and biological intuition on the importance of sampling is vital for designing cost effective management programs for biological invasions. Therefore, we developed a general model, ignoring details that vary among organisms. The core of the sampling problem is the following trade-off: when the invader is rare, it is costly to find, but relatively cheap to control. When the invader is abundant, it is easy to find, but costly to control. Using this trade-off, our model captures the essence of invasive population dynamics and management to propose clear rules of thumb for when intense early sampling is important.

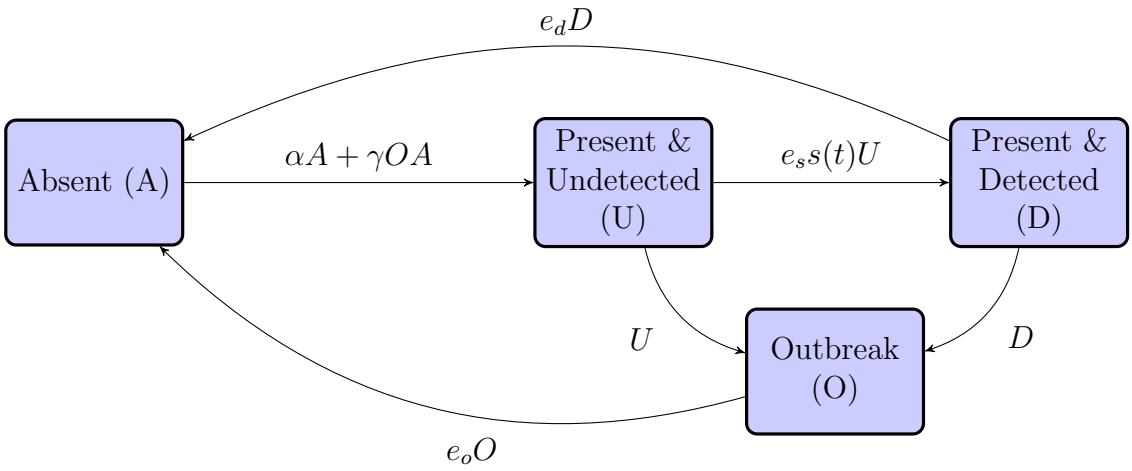

Figure 2.1: A flow diagram for the ecological model

Our model (see Fig. 2.1) considers a landscape of infinitely many patches. In each patch, the invasive may be absent, present but undetected, detected, or present at such high densities that no sampling is required to detect it; we call a patch in the last state an Outbreak. The state variables, $A(t), U(t), D(t)$, and $O(t)$, are the proportion of patches in the Absent, Undetected, Detected and Outbreak states at time t, respectively. In the absence of control, Undetected and Detected patches transition into Outbreaks due to growth of the invasive population. We rescale the model so that one time unit is the average time it takes for an Undetected or Detected patch to transition into an Outbreak. We assume Outbreak patches infect Absent patches at rate $\gamma A(t)O(t)$, via the law of mass action. Therefore, γ is the local spread rate, defined as the average number of patches infected by a single outbreak, over the average lifespan of an Undetected patch, when nearly all other patches are Absent. Absent patches can also be infected by an outside source at a constant rate α. The presence of invasives in Undetected

patches is detected via sampling at rate $e_s s(t)$, where e_s is sampling efficacy and $s(t)$ is the *per-patch* sampling effort deployed in Absent and Undetected patches at time t. Detected patches are eradicated at rate e_d. Outbreak patches are also eradicated, but at a slower rate, e_o, since eradicating large populations is often very difficult. These assumptions yield:

$$\begin{aligned}
\frac{dA}{dt} &= e_o O + e_d D - \alpha A - \gamma O A \\
\frac{dU}{dt} &= \alpha A + \gamma O A - e_s s(t) U - U \\
\frac{dD}{dt} &= e_s s(t) U - e_d D - D \\
\frac{dO}{dt} &= U + D - e_o O.
\end{aligned} \tag{2.1}$$

2.2.2 Economic model

The assumed goal for the manager is to choose sampling effort, $s(t)$, over a time interval of length T, to minimize the total cost of the invasion, including the costs of damage by the invader, sampling and control. We assume s_{max} is the maximum amount of sampling effort a manager can deploy at any given time. Let k_u be the cost of the invader's damage in an Undetected patch, and k_o, and k_d be the sum of the costs of the invasive's damage and the the manager's eradication effort in Outbreak and Detected patches, respectively. Let $f(s)$ be the per-patch cost of deploying s units of sampling effort. All future costs are discounted at rate δ, meaning one dollar now is worth $e^{-\delta t}$ dollars t time units in the future (δ can be thought of as an interest rate). Therefore, the total discounted cost of the invasion, per-patch, is

$$J = \int_0^T e^{-\delta t} \left[k_u U + k_o O + k_d D + f(s)(A + U) \right] dt. \tag{2.2}$$

We assume $f(s) = k_s s + \epsilon s^2$. If $\epsilon = 0$, k_s is just the per unit cost of sampling. If ϵ is small, then the cost of sampling is approximately linear, until sampling effort reaches such high levels that the scarcity of supplies or labor drives up per-effort costs. In most cases ϵ would be much smaller than k_s so that the quadratic term is negligible for sampling rates a manager typically deploys in the field. However, for sampling programs that require skilled labor or specialized equipment, ϵ could be considerably greater than zero due the diminishing supply and increasing demand for qualified employees. The inclusion of the quadratic term is also mathematically convenient, as it guarantees the existence of an optimal solution.

To find the sampling strategy through time, $s(t)$, that minimizes the cost of the invasion, J, we use optimal control theory (Lenhart and Workman, 2007). Optimal control theory is a set of methods for determining the best action to take at each moment in time, in a way that minimizes total costs, which include the cost of taking an action, the cost of the system state changing in response to that action, and the cost of future actions that must be taken due to the resulting system state (see section 5.1 for the full mathematical analysis).

2.2.3 Possible sampling strategies

Two types of constant strategies have been used to develop surveillance plans in the literature, optimal constant sampling and optimal equilibrium sampling, and so we compare the costs of deploying these strategies to the optimal time varying sampling strategy, $s(t)$. We define *optimal constant sampling* as the most cost

effective sampling effort, if sampling effort is not allowed to change in time (i.e. the value of s that minimizes J if $s(t) \equiv s$).

For any constant sampling effort $s(t) \equiv s$, the proportion of patches in each state will approach and remain at an equilibrium depending on s. We call the value of s that minimizes the total cost of maintaining this equilibrium *optimal equilibrium sampling* and we refer to the corresponding proportion of Undetected and Outbreak patches as the *optimal equilibrium*. The optimal equilibrium is non-zero (i.e., the invasive is not completely eliminated). Because sampling is less and less cost effective when the pest is rare, complete elimination is not economically optimal.

Since the *optimal equilibrium strategy* is a specific type of constant strategy, optimal equilibrium sampling will always be at least as costly as optimal constant sampling. For most of our analysis we will compare the optimal time varying strategy to the optimal constant strategy, and not the equilibrium strategy, since any observed difference in costs would only be magnified by comparing our strategy to equilibrium sampling. However, equilibrium sampling is important, not only because past studies have recommended management based on this calculation but also because it will help us describe the optimal time varying sampling policy.

2.2.4 Parameterization

As an illustrative example we consider the management of gypsy moth, *Lymantria dispar*, an invasive forest pest in the United States that has spread across the northeast. Gypsy moth causes massive defoliation, resulting in economic damage due to tree mortality and also the decline of native insect and bird populations

(Thurber et al., 1994; Redman and Scriber, 2000). It is not well established on the west coast, and Washington, Oregon and California spend millions of dollars per year sampling to detect and eradicate isolated populations. We used data from the Washington State gypsy moth eradication program and the largest successful eradication in the United States, in Lane County Oregon, to estimate e_s, k_s, k_o, k_u, e_o and k_d, as displayed in table 2.1. See section 5.2 for details on the parameterization. Note, our general model should not be used to develop specific management strategies for gypsy moth in the field, as it is too simple to provide specific protocols. However, gypsy moth provides us a baseline parameterization, grounded in reality, and we use this parameterization to demonstrate when intense early sampling is most important for cost effective invasive species management, and especially how these differences are magnified by changes in the cost and effectiveness of management and how the invader spreads.

Table 2.1: variables and parameters

Symbol	**Description**	***L. dispar* baseline**	**Parameter ranges tested**
$A(t)$	proportion of patches where the invader is absent at time t	-	-
$U(t)$	proportion of patches where the invader is present but undetected at time t	-	-
$O(t)$	proportion of Outbreak patches at time t	-	
$s(t)$	per-patch sampling effort in Absent and Undetected patches at time t	-	-
s_{max}	maximum possible sampling effort	3960 traps	150-5000
γ	rate at which Outbreaks infect new patches	varies	0 - 10
α	rate at which absent patches are colonized from an outside source	varies	0 - 0.1
e_s	the rate at witch a trap detects an Undetected patch	0.56	0.01 - 1
e_o	the rate at witch Outbreaks are eradicated	3.25	0.1 - 6
e_d	the rate at witch Detected patches are eradicated	13	6 - 156
k_u	cost of damage per undetected patch per unit time	30.3 thousand USD $\cdot$ patch^{-1}	0 - 400,000 USD
k_o	cost of damage and control per Outbreak patch per unit time	88.8 million USD $\cdot$ patch^{-1}	2,000 - 200 mil USD
k_d	cost of damage and control per Detected patch per unit time	582.5 thousand USD $\cdot$ patch^{-1}	50,000 - 800,000 USD
k_s	cost per unit of sampling effort	646 USD $\cdot$ trap$^{-1}\cdot$ patch^{-1}	50 - 2,000 USD
T	length of time the invasive is being managed	5 (i.e. 65 years)	5
ϵ	weighting of quadratic sampling cost	0.01	0 - 25
δ	discount rate	0.13	0 - 1

2.3 Results

The optimal strategy, regardless of the parameters, is to initially sample such that the population is quickly driven to the optimal equilibrium, then sample at a constant rate to maintain this equilibrium pest density, ultimately ceasing to sample as the end of the management period approaches (see Fig. 2.2a for a typical example). Ceasing to sample near the end occurs because a manager in the model has to pay costs for sampling but does not get the benefit from the resulting prevention of the invasive's spread and damage after time T. This is an artifact of finite-time control problems and we ignore it for the rest of this paper.

In most situations the initial approach towards equilibrium is characterized by intense early sampling, followed by a drastic reduction in sampling effort (see Fig. 2.2a, black solid curve, for a typical strategy, and Fig. 2.2bc for the corresponding population dynamics). However, the initial sampling intensity and the amount of money saved by deploying such "early detection" strategies, depends on four main factors: (1) the rate at which the invasive spreads within the managed area, (2) the cost of outbreaks and sampling, (3) the efficacy of sampling and eradicating outbreaks, and (4) the initial frequencies of Undetected and Outbreak patches.

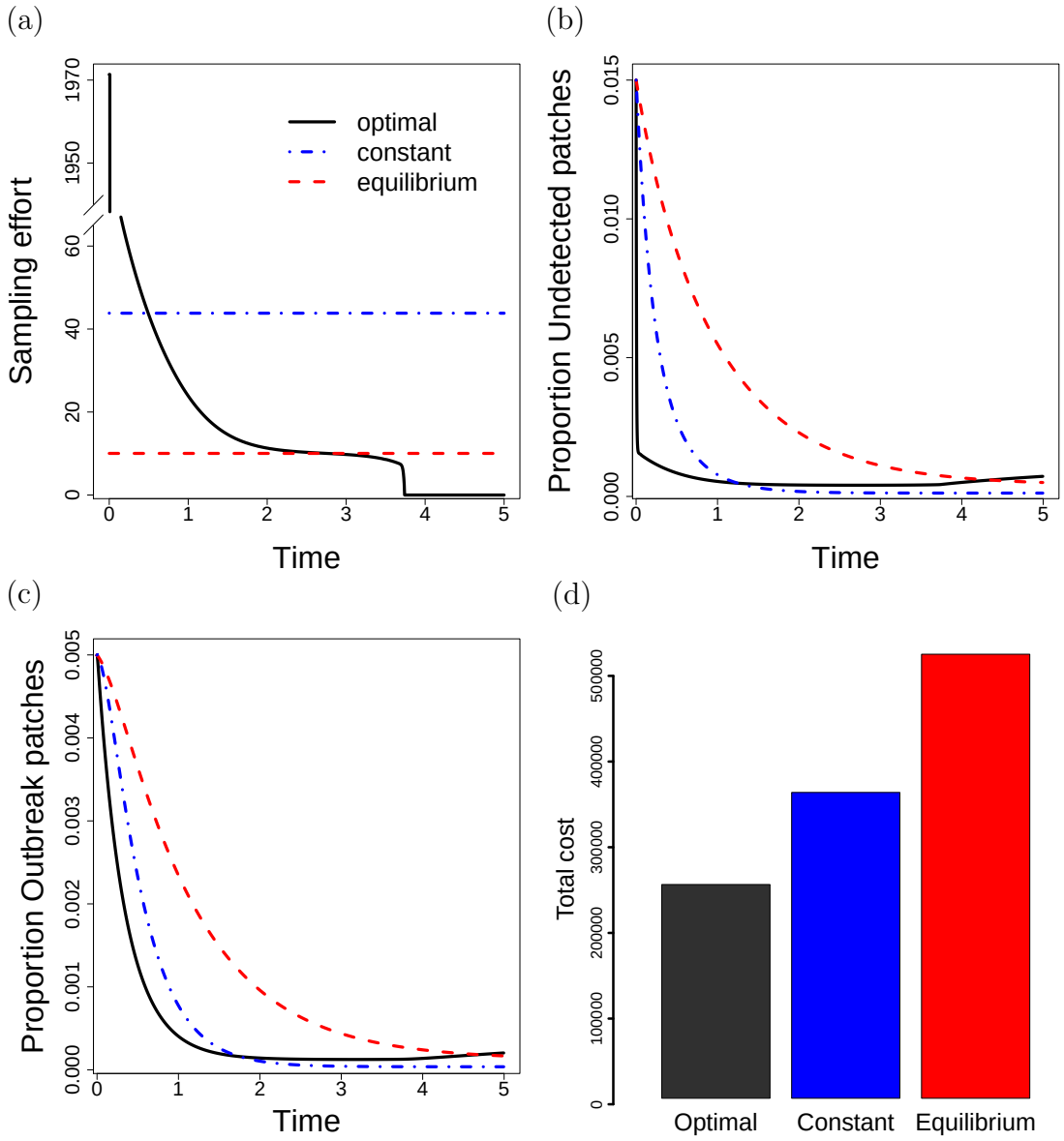

Figure 2.2: (a) Per-patch sampling effort as a function of time for, the time varying strategy (solid black), the equilibrium strategy (dashed red), and the best constant strategy (dot dashed blue). (b) The corresponding dynamics of the proportion of Undetected patches and (c) Outbreaks. (d) The total per-patch cost, in USD, of deploying the optimal intense early sampling strategy, the best constant strategy and the optimal equilibrium sampling strategy. One time unit is 13 years, corresponding to a 65 year management window. Parameters are $\alpha = 0.0001, \gamma = 2, s_{max} = 1980$, the rest as in Table 2.1.

Spread: Fixing all parameters to the values estimated for gypsy moth, but varying both α, the introduction rate, and γ, the local spread rate, we find that intensive early sampling is important if established local populations spread the invasive much more frequently than it is arriving from an outside source (high γ and low α, see Fig 2.3ab compared to Fig 2.3cd). Intense early sampling pays off because it prevents Undetected patches from transitioning into Outbreaks, which are the primary source of new infections when introductions from an outside source are infrequent. In this case high initial sampling can save a manager over 40% of the total invasion cost compared to a manager using optimal constant sampling (Fig. 2.3a).

While the total cost savings of using intense early sampling is bigger for large local spread rates (compare the total difference between the black and gray bars in Fig. 2.3a to the difference in Fig. 2.3b), proportionally the cost benefit decreases. This is because increasing the local spread rate increases the total cost under both strategies much more than it increases the cost savings from early detection.

We note that with a slow introduction rate the total savings is similar regardless of how quickly the manager is able to eradicate detected patches (compare the the absolute difference in the heights of the black and gray bars on the right to the difference on the left in Fig. 2.3ab). However, because the total cost of management is highest for when eradication is slow, the *proportional* cost savings is lower in this case. When the eradication of detected patches is fast there is both a large proportional and total cost savings.

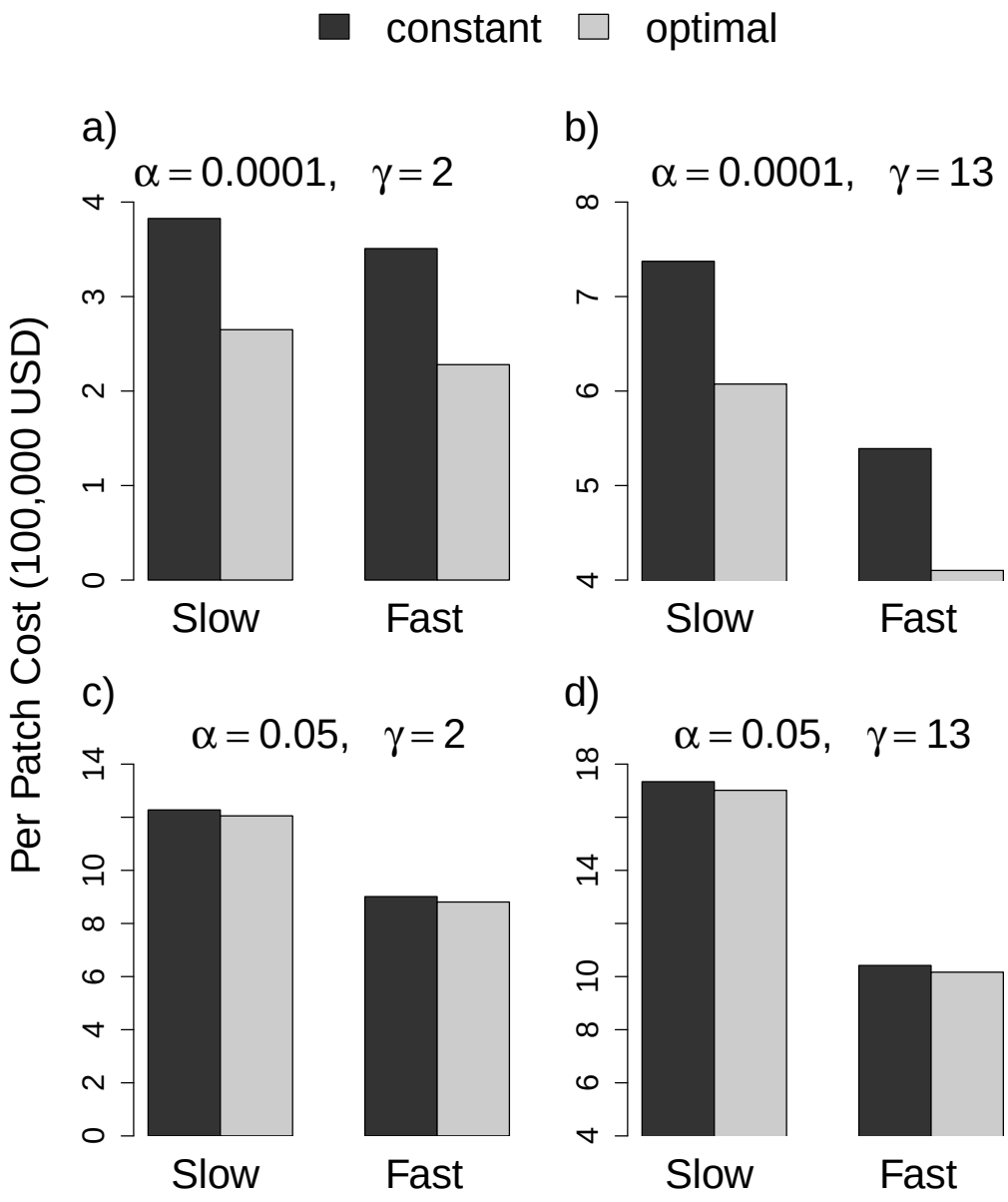

Figure 2.3: Per patch cost of the best constant sampling (black bar) and intense early sampling (gray bar) strategies, for (a) low introduction and local spread rates, (b) low introduction and high local spread rates, (c) high introduction, and low local spread rates and (d) high introduction and local spread rates. (a-d) The bars on the left are for slow management, an average Detected patch eradication delay of one year and the bars on the right are for fast management, a four month delay. Note that in (b) and (d) the cost axis does not start at zero. Other parameters are in Table 2.1.

If new local infestations are the result of frequent introductions from an outside source (high α and low γ) then constant sampling strategies can be almost as cost effective as intense early sampling protocols (see Fig. 2.3cd). In this case sampling and eradication prevent the manager from accruing the added cost of Undetected patches turning into outbreaks, but they do not significantly contribute to preventing new infestations, since most newly colonized patches result from introductions that are out of the manager's control.

Costs: There are four costs in our model, but the cost of sampling and the cost of Outbreak patches are the most crucial for determining when intense early sampling strategies greatly reduce the total cost of an invasion. When fixing the parameters e_d, e_s, and e_o to match the baseline values for gypsy moth management and randomly varying all four cost parameters simultaneously using Latin Hypercube Sampling (McKay et al. (1979), see Table 2.1 for parameter ranges), nearly all the variation in the relative cost of deploying constant versus intense early sampling is explained by the sampling and Outbreak costs, k_s and k_o (Fig. 2.4ab). The cost of damage in Undetected patches and the cost of managing small detected populations is relatively unimportant (see Fig. 5.1ab on pg. 115).

When a unit of sampling effort is nearly as costly as managing an Outbreak, the manager should not sample at all in both the time varying and constant case. Also, if the cost of a single unit of sampling is close to zero, sampling rates are high for the constant strategy and hence nearly match intense early sampling protocols. Therefore, only for a wide range of intermediate, sampling to Outbreak cost ratios, is there great proportional benefits to using intense early sampling (Fig. 2.4b).

In the gypsy moth parameterization, if we assume low introduction rates,

there is a wide range of sampling to Outbreak cost ratios, spanning multiple orders of magnitude, for which there is at least a 15 percent reduction in costs when using intense early sampling strategy (Figs. 2.4b, and 5.1c on pg. 115). For example, with a trap cost of 50 USD, early sampling is important for Outbreak costs ranging between 50 thousand to five billion USD per year. Note that the cost of sampling and the cost of managing outbreaks, based on values reported in the literature, are at levels that come close to maximizing the importance of early sampling, as long as the gypsy moth introduction rate from an outside source is low (red line in Fig. 2.4b).

Discounting future costs always reduces optimal sampling because the cost of sampling is immediate, but the benefits of sampling accumulate in the future. Therefore, it is not surprising that high discount rates reduce the importance of early sampling (Fig. 2.4c).

Increasing ϵ magnifies the quadratic cost, making sampling most expensive when sampling effort is already high. This reduces the importance of intense early sampling, but the effect is small unless ϵ is large enough to have a have a major effect on costs even when sampling effort is substantially below s_{max} (Fig. 2.4d).

Efficacy of sampling and eradication of Outbreaks: The importance of early sampling is maintained for a wide range of sampling efficacies (Fig. 2.4e).

The outbreak eradication rate can also affect the importance of early sampling (Fig. 2.4f). In terms of *total* cost savings, if eradicating outbreaks is slow, it is especially important to sample early. However, the *ratio* of the cost of using a constant strategy to the cost using an early sampling strategy, increases with the

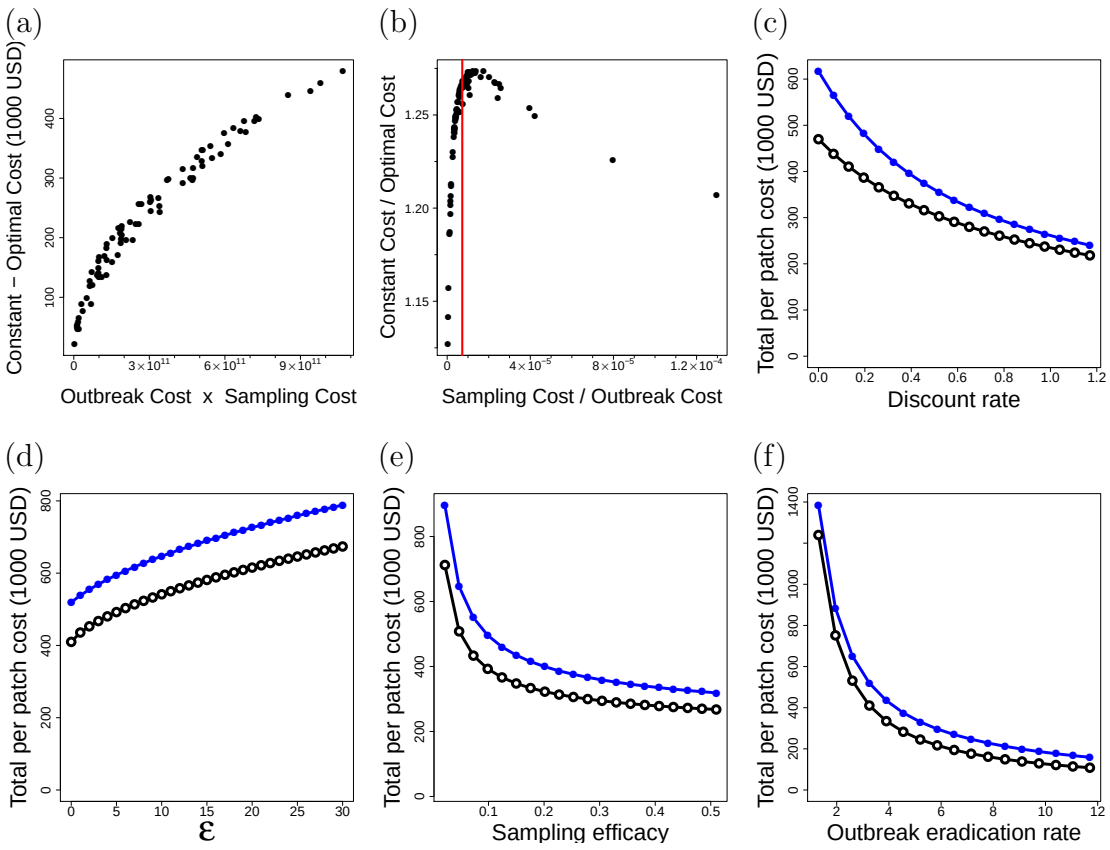

Figure 2.4: (a) The total cost savings of deploying the intense early sampling strategy instead of the constant strategy as a function of the product of sampling and Outbreak management costs. (b) Relative cost of the constant sampling and intense early sampling strategies, as a function of the ratio of sampling cost to Outbreak cost. The red line corresponds to the baseline values in table 2.1. For (ab) we varied all cost parameters via Latin Hypercube Sampling. (c) The total per-patch cost of deploying the constant strategy (blue filled circles) and the intense early sampling strategy (open black circles) as a function of the discount rate, δ (c), quadratic cost penalty, ϵ (d), and sampling efficacy, e_s (e), and the Outbreak eradication rate, e_o (f). Parameters are $\alpha = 0.0005$, $\gamma = 2$, and the rest as in table 2.1.

increased Outbreak eradication rate (Fig. 2.4f).

When intense early sampling isn't optimal: Early detection strategies will be more cost effective than constant strategies unless the initial proportion of Undetected and Outbreak patches is below the optimal equilibrium. Theoretically, in such cases, the manager waits until their is a critical density of Undetected patches before deploying any sampling effort (see Fig. 5.2ab on pg. 116).

This case is likely rare because, for the majority of reasonable parameter values, the optimal equilibrium is very close to zero Undetected and Outbreak patches. Therefore, as long as the invasive is known to exist somewhere in the managed area, it is optimal to sample heavily in the beginning of the management period. The only time this is not the case is if sampling is so ineffective that high sampling effort does not reduce the population to low levels (Fig. 5.2c on pg. 116). In this case, either no sampling is ever deployed or the equilibrium proportion of infected patches is so high that the approach towards equilibrium is characterized by zero initial sampling, followed by a gradual increase in sampling effort as the pest becomes abundant (Fig. 5.2c on pg. 116).

Unknown initial frequency of the invasive: When a manager first starts to develop sampling protocols, the extent of the invasion is usually unknown. There are two likely scenarios (1) there is reason to believe an invader is present but it has not been detected or (2) an Outbreak has been reported but it is unclear if this is an isolated population or it has already infected other patches. In case one, even if the invasive is present with small probability, early detection strategies can still perform better, on average, than constant strategies. For example, suppose that a manager (correctly) estimates that there is probability p of the invasive being present in three out of 200 patches in the managed area, and otherwise the invasive

is completely absent. Given the cost parameters from the gypsy moth example and with $\gamma = 2$ and $\alpha = 0.0005$, even if p is as low as 0.2 it is still better to deploy intense sampling effort early than to sample at the constant or equilibrium rate (Fig. 2.5a).

In case (2), where an outbreak is detected but the number of Undetected patches is unknown, intense early sampling can be beneficial, even when there are no other infected patches to start with. For example, consider a landscape with initially one Outbreak out of 200 patches. In addition it has three Undetected patches with probability p and no Undetected patches with probability $1 - p$. Given the cost parameters from the gypsy moth example and with $\gamma = 2$ and $\alpha = 0.0005$, even if $p = 0$, it is still more cost effective to deploy intense early sampling effort than it is to sample at the best constant rate (Fig. 2.5b). The reason for this is that with an Outbreak patch initially present, even though the intense early sampling strategy overspends when no Undetected patches are initially present, it is able to prevent a large initial buildup of Undetected patches that spread from the Outbreak before successful Outbreak eradication (Fig. 2.5c).

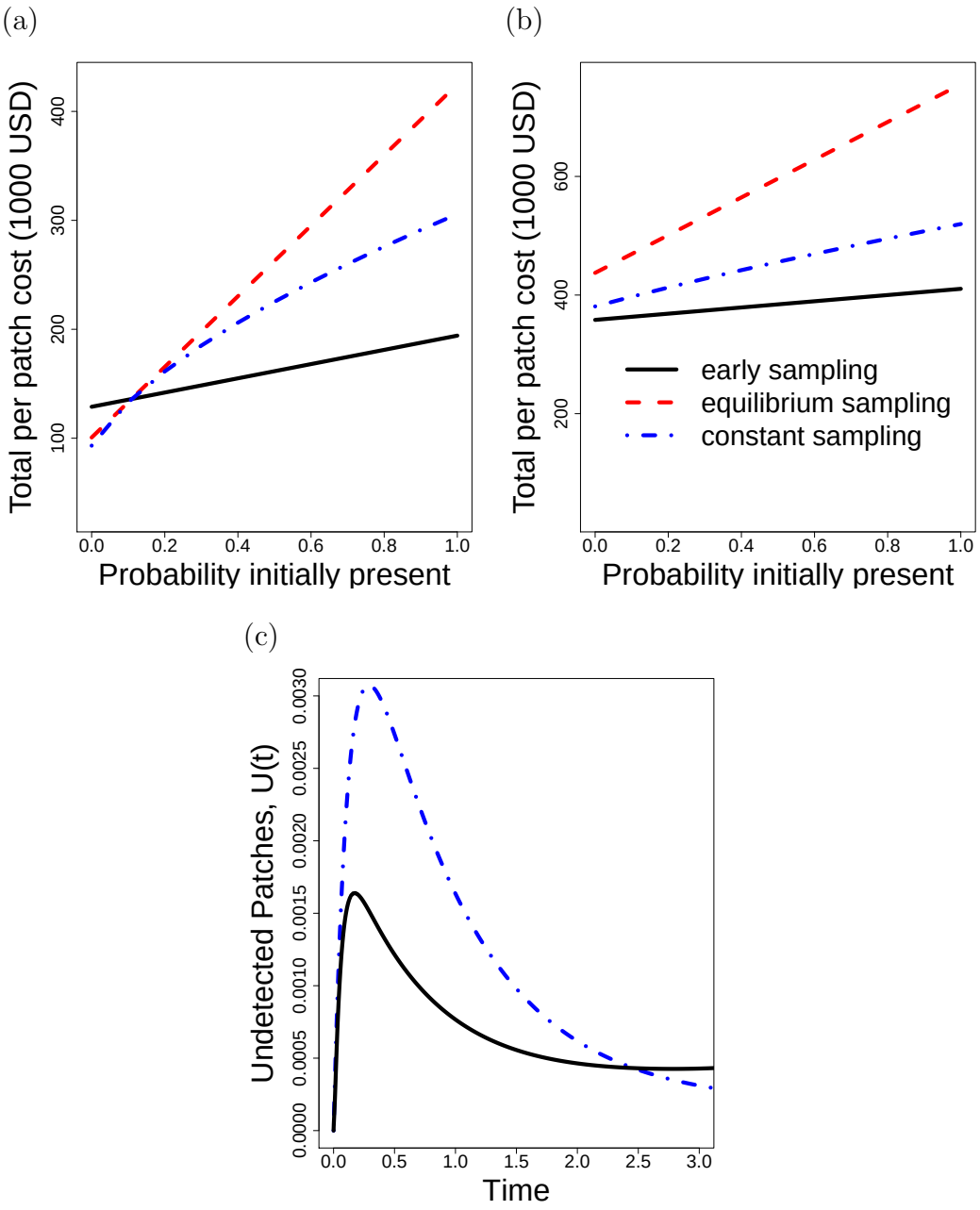

Figure 2.5: (a) The expected per-patch cost of management, assuming the landscape is initially 1.5% Undetected patches with probability p and completely absent of the invader with probability $1-p$, under the optimal equilibrium (dashed red line), the best constant (dot-dashed blue line), and the intense early sampling (black solid line) strategy, as a function of p. (b) The expected per-patch cost of management assuming an initial landscape with 0.5% Outbreaks and additionally, with probability p, 1.5% Undetected patches, as function of p. (c) The corresponding Undetected patch dynamics as a function of time when there is initially 0.5 % Outbreaks and no Undetected patches under the best constant strategy (dash-dotted blue line) and the intense early sampling strategy (solid black line). The parameters are $\gamma = 2, \alpha = 0.0001$, and the rest as in 2.1.

2.4 Discussion

In this paper we showed that intense early sampling protocols are key to cost effective management for invasive species with low introduction rates and high spread rates. However, when introduction from an outside source dominates local spread, the best constant effort strategies perform near optimally. Note we are not saying that sampling effort should be low when introduction rates are high. When introduction rates are high, sampling effort should be high during the entire management program, but there is less of a cost benefit of increasing initial sampling effort over the optimal constant level.

When a manager is considering carrying out an intense initial search for the invader, on top of the constant sampling she already plans to do, she should ask the following question: "If I find a new infestation, is it more likely that this new population is the result of spread from somewhere else in my management area, or is it more likely the result of an independent introduction?"

In many cases, an invasion results from infrequent introduction events. For example, it is hypothesized that the entire gypsy moth invasion can be traced back to a single person accidentally releasing them from his residence in Massachusetts in 1869. At the moment when these moths were first reported to be a nuisance, the introduction rate was probably close to zero, and therefore intense early sampling would have been desirable. Unfortunately, a management program wasn't enacted until more than twenty years after this introduction. The *Anoplophora glabripennis*, Asian longhorned beetle, invasion at the country scale, is another example that might benefit from intense early sampling, since its introduction rate into several countries is very low (see table 2 of Haack et al. (2010)).

The management of species that invade fresh water systems may also benefit from intense early sampling because local spread within a lake or network of lakes, due to boat traffic and natural currents, can be much faster than the introduction and establishment rate from an outside source. For example, *Hydrilla verticillata*, is an invasive aquatic weed in the US that can quickly reproduce and spread via stolons, seeds, fragmentation and turions (Langeland, 1996). Once a small outbreak has been detected within a lake, the remaining habitable area within the lake should be sampled intensely.

The spatial scale at which the invasive is being managed should be considered when deciding whether intense early sampling is important. For the management of an invasive species at a national or global scale, the introduction rate may only incorporate infrequent spread through international transportation and trade. However, a manager in charge of a state, county, city, national park or farm will incorporate spread that would be considered "local" at a national scale into the introduction rate. Introductions include spread from populations the manager cannot control and the local spread rate includes dispersal between populations the manager can eradicate.

The issue of spatial scale means that intense early sampling strategies will not be crucial to reduce costs for all invasive species. In the case of gypsy moth management in the mid west and on the west coast of the United States, the introduction rate from the east coast is very high due to frequent, loosely regulated travel within the country. So our case study confirms that restrictions in past gypsy moth models to constant strategies (Sharov and Liebhold, 1998; Bogich et al., 2008; Epanchin-Niell et al., 2012) should produce reasonably cost efficient sampling rates. Since these sampling rates are much lower than what is deployed in Washington

(Bogich et al., 2008), it is possible that Washington's managers are sampling too intensely.

In California, Epanchin-Niell et al. (2012) found that the best equilibrium sampling effort closely matched the statewide trap densities deployed in 2010. However, such strategies still recommend 42 percent less sampling than California's historic average trap density prior to 2008 (Bogich et al., 2008). While there are many potential explanations for this, including random chance or reduced operating budgets, another possibility is that California has been decreasing sampling effort over time, towards optimal equilibrium sampling, which our model suggests is optimal.

Scientists are now recommending that natural resource management agencies develop surveillance programs guided by optimal constant sampling strategies (Epanchin-Niell et al., 2014). While such optimization models add objectivity and potentially improved outcomes, we caution that such strategies can be cost inefficient compared to intense early sampling. Since it is often intractable to do time dependent optimization on complicated models used for real world management problems, it might be beneficial to augment constant sampling effort, resulting from static optimization methods, with an intense pulse of early sampling.

Along with previous work on the optimal surveillance of invasive species (Mehta et al., 2007; Bogich et al., 2008; Hauser and McCarthy, 2009; Haight and Polasky, 2010; Homans and Horie, 2011; Epanchin-Niell et al., 2012; Horie et al., 2013; Epanchin-Niell et al., 2014; Rout et al., 2014), we emphasize weighing the trade-offs between the cost of sampling and future costs resulting from damages and more expensive management actions. For any invasive species, it will be less costly to manage a small population than an outbreak. However, previous mathematical

work has underplayed the importance of early sampling and therefore undervalued the utility of extensive search in cases where new infestations are caused mostly by local spread. The benefits of intense early sampling in such situations can help explain why managers tend to sample more than what past studies have suggested is optimal and why government agencies list "early detection" as one of the key components of invasive species management.

CHAPTER 3

OPTIMAL ESCAPEMENT FOR STAGE STRUCTURED FISHERIES WITH ENVIRONMENTAL STOCHASTICITY

Abstract

Stage structured population models are commonly used to understand fish population dynamics and additionally for stock assessment. Unfortunately, there is little theory on the optimal harvest of stage structured populations, especially in the presence of stochastic fluctuations. In this paper, we find closed form optimal equilibrium escapement policies for a three dimensional, discrete time, stage structured population model with linear growth, post-harvest nonlinear recruitment, and stage specific pricing and extend the analytic results to structured populations with environmental stochasticity. When only fishing reproductive adults, stochasticity does not affect optimal escapement policies. However, when harvesting immature fish, the addition of stochasticity can increase or decrease optimal escapement depending on the second and third derivative of the recruitment function. For logistic recruitment, stochasticity reduces optimal immature escapement by a multiplicative factor of one over one plus the variance of the environmental noise. Using hard clam, *Mercenaria mercenaria*, as an example and assuming Beverton-Holt recruitment, we show that optimal fishing of hard clam targets the immature stage class exclusively and that environmental stochasticity should increase optimal escapement.

3.1 Introduction

Fisheries biologists, managers and economists widely recognize that traditional one dimensional bioeconomic models are too simple for developing management guide-

lines for the majority of real-life fisheries (Clark, 2010), as policies derived from such models can drastically reduce profits and stock sizes when naively applied to age structured populations (Tahvonen, 2008). While determining optimal age specific harvest policies is a classic problem in bioeconomics (Clark et al., 1973; Beddington and Taylor, 1973; Rorres and Fair, 1975; Reed, 1980; Getz, 1980; Gurtin and Murphy, 1981), and an active area of both theoretical and applied research (Tahvonen, 2009; Diekert et al., 2010; Skonhoft et al., 2012; Da Rocha et al., 2013; Tahvonen et al., 2013; Kanik and Kucuksenel, 2013; Quaas et al., 2013; Skonhoft and Gong, 2014), the effect of stage structure and environmental stochasticity on optimal fisheries management is poorly understood.

Stage-structured models are often used to understand fish population dynamics and perform stock assessment (Liu et al., 2002; Swain et al., 2009). It is usualy more convenient for managers to obtain data on fish size or life stage rather than age. Techniques for aging organisms can be expensive and time consuming and in extreme cases logistically infeasible (Bergh and Johnston, 1992). In addition, fish prices are often based on discrete size classes or life stages (Reddy et al., 2013; Bricelj et al., 1980). While developing optimal harvest rules for size and stage structured populations can potentially improve fisheries management, it is more challenging to solve for optimal strategies in this framework due to the lack of sparsity in the equations for stock dynamics.

Past studies have simplified the problem by limiting transitions between stage classes (Getz and Haight, 1989; Tahvonen, 2014) or using continuous time models, including two dimensional ordinary differential equations (e.g. (Jing and Ke, 2004)) and partial differential equations (Botsford, 1981; Busoni and Matucci, 1997). However, fisheries biologists usually use discrete time models for stock

assessment (Deriso, 1999) and variability between individuals within a population can lead to a wide range of stage transitions, previously unexplored with respect to optimization.

Tahoven's model Tahvonen (2014) is the most similar to our deterministic setup, but differs in a few key ways. We assume that harvest occurs prior to growth and recruitment, as is usually the case for migrating fish populations such as eel and salmon (De Leo and Gatto, 2001; Nickelson and Lawson, 1998) and that individuals can skip stages. However, the biggest difference between our two approaches is that we consider the addition of environmental stochasticity.

While the effect of environmental stochasticity on optimal harvest has been widely studied for one dimensional bioeconomic models (e.g. (Reed, 1979)), little is known about how stochasticity affects optimal harvest in structured populations. Of the few studies that exist, stochasticity is typically only included in the form of random recruitment, and usually independent of spawning biomass (Getz and Haight, 1989; Da Rocha et al., 2013). In addition, solutions heavily rely on numerical simulation and error-bound approximation (Getz and Haight, 1989; Mendelssohn, 1978).

In this paper, to our knowledge, we provide the first analytic optimal constant stationary escapement solution for a demographically structured population model with endogenous, nonlinear recruitment and environmental stochasticity affecting all classes. We find that with the addition of environmental stochasticity, the optimal escapement of reproductive adults remains unchanged from the deterministic case, if harvest occurs prior to recruitment. However, in the case of immature harvest, fishing should either be more aggressive or conservative than the deterministic case depending on the second and third derivatives of the recruit-

ment function. For example, if the recruitment function is logistic, escapement should decrease by a factor of one over one plus the variance of the environmental noise. We use historical data from New York state's hard clam fishery to provide a concrete example of our theoretical results.

3.2 The deterministic model

Consider a harvested fish population, with stage or size structured dynamics,

$$\begin{aligned} B_{1,t+1} &= R(B_{3,t} - h_t) + a_{11}B_{1,t} \\ B_{2,t+1} &= a_{21}B_{1,t} + a_{22}(B_{2,t} - \eta_t) \\ B_{3,t+1} &= a_{31}B_{1,t} + a_{32}(B_{2,t} - \eta_t) + a_{33}(B_{3,t} - h_t), \end{aligned} \tag{3.1}$$

where $B_{1,t}$, $B_{2,t}$, and $B_{3,t}$ are the biomass of juvenile (stage 1), immature (stage 2) and adult (stage 3) fish at time t, respectively. The Juvenile stage consists of fish too small to reproduce or catch. The immature stage consists of all fish large enough to catch but still cannot reproduce. At time t, h_t and η_t units of biomass are harvested from the adult and immature fish population. The remaining fish survive and grow, where a_{ij} is the average amount of biomass gained in stage i, at time $t+1$, per unit of biomass that escaped harvest in stage j at time t. Adults that escape harvest, reproduce, generating offspring with total biomass described by a bounded, positive, concave, density dependent recruitment function $R(\sigma_t)$, where $\sigma_t = B_{3,t} - h_t$ is the spawning biomass at time t and $R(0) = 0$. We can write the model in matrix notation as

$$\hat{B}_{t+1} = A(\hat{B}_t - \hat{h}_t) + \hat{R}_t \tag{3.2}$$

where

$$\hat{B}_t = \begin{pmatrix} B_{1,t} \\ B_{2,t} \\ B_{3,t} \end{pmatrix}, A = \begin{pmatrix} a_{11} & 0 & 0 \\ a_{21} & a_{22} & 0 \\ a_{31} & a_{32} & a_{33} \end{pmatrix}, \hat{h} = \begin{pmatrix} 0 \\ \eta_t \\ h_t \end{pmatrix}, \hat{R}_t = \begin{pmatrix} R(B_{3,t} - h_t) \\ 0 \\ 0 \end{pmatrix},$$

We wish to optimize total discounted revenue, where revenue is a linear function of harvest,

$$\max_{h_t, \eta_t} \left\{ \sum_{t=0}^{\infty} \rho^t (p_3 h_t + p_2 \eta_t) \right\}, \tag{3.3}$$

with p_2 and p_3, the price per unit biomass of immature and adult fish respectively and $\rho = 1/(1+\delta)$ the discrete discount factor, with discount rate δ.

3.3 Analysis of the deterministic model

Proposition 3.1. *The system 3.1, with $\hat{h} = \mathbf{0}$, has a positive equilibrium, $\hat{B}^*$ if and only if*

$$R'(0) > \frac{(1-a_{11})(1-a_{22})(1-a_{33})}{a_{21}a_{32} + a_{31}(1-a_{22})} := c. \tag{3.4}$$

Proof. By simple algebra, if there exists an $x > 0$ such that $R(x) = cx$, then there is a positive equilibrium, $\hat{B}^*$, with $\hat{B}^*_3 = x$. Assume $R'(0) > c$ and define $f(x) := cx - R(x)$. By continuity of R', there exists an $\tilde{x} > 0$, sufficiently small, such that $R(\tilde{x}) > c\tilde{x}$. Hence $f(\tilde{x}) < 0$. Since R is bounded, there exists an $x > \tilde{x}$ such that $f(x) > 0$. Therefore, by the intermediate value theorem, there exists a positive x such that $f(x) = 0$, the solution of which defines the adult biomass equilibrium. The reverse direction follows from writing down the implicit equation for the equilibrium and applying the mean value theorem. □

If inequality (3.4) is not met, small populations fail to persist, even without harvest. For the rest of this paper we assume a slightly stronger inequality is met, namely $R'(0) > (1+\delta)^3 c$, which guarantees that at low densities a fish in the water is worth more than the revenue generated from harvesting that fish. Note, we will also assume that $a_{ii} < 1$ for all $i \in \{1, 2, 3\}$. This allows for individual fish gaining biomass without transitioning to the next stage of their life-cycle. However, due to mortality, the average amount of biomass gained within a stage is not allowed to grow. Without this assumption it is possible for the fish stock to grow unbounded.

We use the method of Lagrange multipliers (pg. 60 of (Clark, 2010)) to solve for the equilibrium optimal harvest policy. The Lagrangian is

$$\begin{aligned}\mathscr{L} = \sum_{t=0}^{\infty} \rho^t \{ & p_3 h_t + p_2 \eta_t + \rho\lambda_{1,t+1}[R(B_{3,t} - h_t) + a_{11}B_{1,t} - B_{1,t+1}] \\ & + \rho\lambda_{2,t+1}[a_{21}B_{1,t} + a_{22}(B_{2,t} - \eta_t) - B_{2,t+1}] \\ & + \rho\lambda_{3,t+1}[a_{31}B_{1,t} + a_{32}(B_{2,t} - \eta_t) + a_{33}(B_{3,t} - h_t) - B_{3,t+1}]\},\end{aligned} \tag{3.5}$$

where $\rho\lambda_{i,t+1}$ is the current value shadow price for $B_{i,t}$, the money someone would pay for a small additional amount of biomass in the ith stage at time $t+1$. Taking the partial derivatives of the Lagrangian,

$$\frac{\partial \mathscr{L}}{\partial B_{1,t}} = \rho^t(\rho a_{11}\lambda_{1,t+1} + \rho a_{21}\lambda_{2,t+1} + \rho a_{31}\lambda_{2,t+1} - \lambda_{1,t}) \tag{3.6}$$

$$\frac{\partial \mathscr{L}}{\partial B_{2,t}} = \rho^t(\rho a_{22}\lambda_{2,t+1} + \rho a_{32}\lambda_{3,t+1} - \lambda_{2,t}) \tag{3.7}$$

$$\frac{\partial \mathscr{L}}{\partial B_{3,t}} = \rho^t(\rho a_{33}\lambda_{3,t+1} + \rho R'(B_{t,3} - h_t)\lambda_{1,t+1} - \lambda_{3,t}) \tag{3.8}$$

$$\frac{\partial \mathscr{L}}{\partial \eta_t} = \rho^t(p_2 - \rho a_{22}\lambda_{2,t+1} - \rho a_{32}\lambda_{3,t+1}) \tag{3.9}$$

$$\frac{\partial \mathscr{L}}{\partial h_t} = \rho^t(p_3 - \rho R'(B_{t,3} - h_t)\lambda_{1,t+1} - \rho a_{33}\lambda_{3,t+1}), \tag{3.10}$$

yields a set of first-order necessary conditions for an interior solution, and therefore, at equilibrium, optimality requires

$$\lambda_1 = \rho a_{11}\lambda_1 + \rho a_{21}\lambda_2 + \rho a_{31}\lambda_3 \tag{3.11}$$

$$\lambda_2 = \rho a_{22}\lambda_2 + \rho a_{32}\lambda_3 \tag{3.12}$$

$$\lambda_3 = \rho a_{33}\lambda_3 + \rho R'(B_3 - h)\lambda_1 \tag{3.13}$$

$$p_2 = \rho a_{22}\lambda_2 + \rho a_{32}\lambda_3 \tag{3.14}$$

$$p_3 = \rho R'(B_3 - h)\lambda_1 + \rho a_{33}\lambda_3 \tag{3.15}$$

$$B_1 = R(B_3 - h) + a_{11}B_1 \tag{3.16}$$

$$B_2 = a_{21}B_1 + a_{22}(B_2 - \eta) \tag{3.17}$$

$$B_3 = a_{31}B_1 + a_{32}(B_2 - \eta) + a_{33}(B_3 - h). \tag{3.18}$$

We note that in almost all cases there is no interior solution to the above system. This is because equations (3.12) and (3.14) imply $\lambda_2 = p_2$, and equations (3.13) and (3.15) imply $\lambda_3 = p_3$, but by equation (3.12) this would mean $p_2 = \rho(a_{22}p_2 + a_{32}p_3)$. So as long as $p_2 \neq \rho(a_{22}p_2 + a_{32}p_3)$ there is no interior equilibrium solution with both $\partial\mathscr{L}/\partial\eta_t = 0$ and $\partial\mathscr{L}/\partial h_t = 0$.

However, it is still possible to have an equilibrium that occurs on the boundary. That is a solution where one harvests all or none of at least one stage class. Consider equations (3.11-3.13,3.15-3.18), that is the system where the shadow prices and biomasses are in equilibrium, and also suppose that $\partial\mathscr{L}/\partial\eta_t < 0$ (which form the Khun-Tucker conditions, see pg. 61 in (Clark, 2010)). In this case, $\eta_t = 0$ and there is no harvesting immature fish. From equations (3.13) and (3.15), we have

$$\lambda_3^* = p_3, \tag{3.19}$$

and hence with equations (3.11) and (3.12) we have

$$\lambda_2^* = \frac{\rho p_3 a_{32}}{1 - \rho a_{22}}, \tag{3.20}$$

$$\lambda_1^* = \frac{\rho^2 p_3 a_{21} a_{32} + \rho p_3 a_{31}(1 - \rho a_{22})}{(1 - \rho a_{11})(1 - \rho a_{22})}. \tag{3.21}$$

With the equilibrium shadow prices the optimal escapement of adult fish, such that $\partial \mathscr{L} / \partial h_t = 0$, is given by

$$R'(\sigma^*) = \frac{(1 - \rho a_{11})(1 - \rho a_{22})(1 - \rho a_{33})}{\rho^3 a_{21} a_{32} + \rho^2 a_{31}(1 - \rho a_{22})}. \tag{3.22}$$

Because R is assumed to be concave on $(0, \infty)$, R' is monotonic decreasing on $(0, \infty)$. Therefore, if a positive solution to (3.22) exists, it is unique. We also note that when the shadow prices are as in (3.19)

$$\frac{\partial \mathscr{L}}{\partial \eta_t} = \frac{\rho^t}{1 - \rho a_{22}} [p_2 - \rho(a_{22} p_2 + a_{32} p_3)], \tag{3.23}$$

which is negative if

$$\rho(a_{22} p_2 + a_{32} p_3) > p_2. \tag{3.24}$$

This condition means the discounted value of immature fish, as a result of survival and growth, is greater than the marginal value of harvesting immature fish today, p_2. In other words, fish are more valuable in the water than on the dock. If this

condition is met, and there is a positive solution for σ^* as calculated in (3.22), we can write the equilibrium biomass as

$$B_1^* = \frac{R(\sigma^*)}{1 - a_{11}} \tag{3.25}$$

$$B_2^* = \frac{a_{21}R(\sigma^*)}{(1 - a_{11})(1 - a_{22})} \tag{3.26}$$

$$B_3^* = \left[a_{31} + \frac{a_{21}a_{32}}{1 - a_{22}}\right] \frac{R(\sigma^*)}{1 - a_{11}} + a_{33}\sigma^*. \tag{3.27}$$

and the harvests as

$$\begin{aligned} h^* &= \frac{a_{21}a_{32}R(\sigma^*)}{(1 - a_{11})(1 - a_{22})} - (1 - a_{33})\sigma^* \\ \eta^* &= 0. \end{aligned} \tag{3.28}$$

From (3.24), it is useful to define

$$\delta_{crit} := \frac{a_{32}p_3}{p_2} + a_{22} - 1, \tag{3.29}$$

the critical discount rate, for which it is equally profitable to harvest adults or immatures. If $\delta < \delta_{crit}$ only adults should be harvested.

The question remains, what is the optimal equilibrium policy if $\delta > \delta_{crit}$? In this case you acquire more money by harvesting immature fish and putting that money in the bank than you would from harvesting them as adults the following year. In such a case we might suspect an interior solution for harvesting immature fish and a boundary solution for harvesting adults. In this case, $\partial\mathscr{L}/\partial\eta_t = 0$, but $\partial\mathscr{L}/\partial h_t < 0$, yielding a steady state system given by equations (3.11-3.14,3.16-3.18). In this system, by equations (3.12) and (3.14)

$$\lambda_2^* = p_2, \tag{3.30}$$

and hence with equations (3.11) and (3.12) we have

$$\lambda_3^* = \frac{p_2(1-\rho a_{22})}{\rho a_{32}}, \tag{3.31}$$

$$\lambda_1^* = \frac{\rho p_2 a_{21} a_{32} + p_2 a_{31}(1-\rho a_{22})}{a_{32}(1-\rho a_{11})}. \tag{3.32}$$

Substituting into (3.13) yields the same adult optimal escapement, σ^*, as in (3.22), and therefore the equilibrium juvenile biomass is still given by (3.25). However,

$$\frac{\partial \mathscr{L}}{\partial h_t} = \rho^t[p_3 - \rho R'(B_3 - h)\lambda_1 - \rho a_{33}\lambda_3] \tag{3.33}$$

$$= \frac{\rho^{t-1}}{a_{32}}[\rho(a_{22}p_2 + a_{32}p_3) - p_2], \tag{3.34}$$

which is negative for $\delta > \delta_{crit}$. This means harvested immature fish are more valuable than harvested adults. So in order to have an adult escapement of σ^*, we harvest immatures, but let $s^* > 0$ escape, so that enough immatures survive and grow to $B_3^* = \sigma^*$ adults. It is possible, if a_{31} and a_{33} are large enough, that $s^* < 0$, which is not feasible. It is also possible to have $s^* = 0$, implying $\eta^* = B_2^*$ with $\sigma^* > 0$, provided a large enough fraction of juveniles skip a stage to become adults ($a_{31} > 0$) and sufficient escaped adults also survive ($a_{33} > 0$). Thus there are two feasible cases.

Case 1. If $\delta > \delta_{crit}$, and $\sigma^* > 0$, as calculated in (3.22), and

$$\frac{a_{31}R(\sigma^*)}{1-a_{11}} < (1-a_{33})\sigma^*,$$

some amount of immature biomass, $s^* > 0$, must be allowed to escape harvest in order to produce enough adults to let σ^* adult biomass escape in the next generation. In other words, not enough juveniles skip the immature life stage and not enough adults survive to create σ^* adult biomass to reproduce in the next generation without the contribution from immatures. In this case, adults are not harvested, yet $B_3^* = \sigma^*$, and therefore,

$$B_3^* = \sigma^* = a_{31}B_1^* + a_{32}s^* + a_{33}\sigma^*. \tag{3.35}$$

Solving for s^* yields

$$\begin{aligned} s^* &= \frac{(1-a_{33})\sigma^*}{a_{32}} - \frac{a_{31}R(\sigma^*)}{a_{32}(1-a_{11})} \\ B_2^* &= \frac{(a_{21}a_{32} - a_{31}a_{22})\,R(\sigma^*)}{a_{32}(1-a_{11})} + \frac{a_{22}(1-a_{33})\sigma^*}{a_{32}}, \\ \eta^* &= \frac{(a_{21}a_{32} + a_{31}a_{22} - a_{31})R(\sigma^*)}{a_{32}(1-a_{11})} - \frac{(1-a_{22})(1-a_{33})\sigma^*}{a_{32}} \\ h^* &= 0. \end{aligned} \tag{3.36}$$

A heat map of total discounted net revenue as a function of adult and immature escapement, for parameters such that the conditions for this case are met, is shown in Fig. 3.2.

Case 2. If $\delta > \delta_{crit}$, and $\sigma^* > 0$, as calculated in (3.22), and

$$\frac{a_{31}R(\sigma^*)}{1-a_{11}} \geq (1-a_{33})\sigma^*,$$

juveniles and adults are contributing enough surplus biomass to the adult stage in the next generation so that σ^* adults can escape, even without any contribution

from immatures. In this case all immatures should be harvested, and some fraction of adults should be harvested as well. However, because we are harvesting from the less valuable adults, adult escapement is not σ^* as calculated in (3.22). In this case, since all immatures are harvested, it helps to write a new reduced system. That is

$$\begin{aligned} B_{1,t+1} &= R(B_{3,t} - h_t) + a_{11}B_{1,t} \\ B_{3,t+1} &= a_{31}B_{1,t} + a_{33}(B_{3,t} - h_t), \end{aligned} \tag{3.37}$$

$$\max_{h_t} \left\{ \sum_{t=0}^{\infty} \rho^t p(h_t + \rho a_{21} B_{1,t}) \right\}. \tag{3.38}$$

The Lagrangian for this new system is

$$\begin{aligned} \hat{\mathscr{L}} = \sum_{t=0}^{\infty} \rho^t \{ & p(h_t + \rho a_{21} B_{1,t}) + \rho\lambda_{1,t+1}[R(B_{3,t} - h_t) + a_{11}B_{1,t} - B_{1,t+1}] \\ & + \rho\lambda_{3,t+1}[a_{31}B_{1,t} + a_{33}(B_{3,t} - h_t) - B_{3,t+1}]\}. \end{aligned} \tag{3.39}$$

Using similar analysis as in the previous model we find that the optimal equilibrium escapement of adults, $\hat{\sigma}^*$ is given by

$$R'(\hat{\sigma}^*) = \frac{p_3(1 - \rho a_{33})(1 - \rho a_{11})}{\rho^2(p_2 a_{21} + p_3 a_{31})} \tag{3.40}$$

and

$$
\begin{aligned}
B_1^* &= \frac{R(\hat{\sigma}^*)}{1-a_{11}} \\
B_2^* &= \frac{a_{21}R(\hat{\sigma}^*)}{1-a_{11}} \\
B_3^* &= \frac{a_{31}R(\hat{\sigma}^*)}{1-a_{11}} + a_{33}\hat{\sigma}^* \\
s^* &= 0, \text{meaning } \eta^* = B_2^* \\
h^* &= \frac{a_{31}R(\hat{\sigma}^*)}{1-a_{11}} + (a_{33}-1)\hat{\sigma}^*
\end{aligned}
\tag{3.41}
$$

3.3.1 Closed form solutions for Logistic and Beverton-Holt recruitment

Depending on the functional form of the recruitment function, $R(\sigma)$, it is possible to obtain closed form solutions for the optimal escapement at equilibrium. For example if R is given by the logistic map with growth rate $r > 1$ and carrying capacity k,

$$
R(\sigma) = r\sigma\left(1 - \frac{\sigma}{k}\right) \tag{3.42}
$$

then, if $\delta < \delta_{crit}$, the optimal adult escapement is given by

$$
\sigma^* = \frac{k}{2r}\left[r - \frac{(1-\rho a_{11})(1-\rho a_{22})(1-\rho a_{33})}{\rho^3 a_{21}a_{32} + \rho^2 a_{31}(1-\rho a_{22})}\right]. \tag{3.43}
$$

If $\delta > \delta_{crit}$ and $a_{31}R(\sigma^*)/(1-a_{11}) < (1-a_{33})\sigma^*$, we harvest no adults and let the amount of immatures that escape harvest be as in (3.35). If $\delta > \delta_{crit}$ and $a_{31}R(\sigma^*)/(1-a_{11}) \geq (1-a_{33})\sigma^*$, then we harvest all of the immatures and let

$$\hat{\sigma}^* = \frac{k}{2r}\left[r - \frac{(1-\rho a_{11})(1-\rho a_{33})}{\rho^2(a_{21}+a_{31})}\right], \tag{3.44}$$

adults escape harvest. Note in this example, the recruitment function can be chaotic depending on the transition coefficients and the growth rate. Our analysis will only hold at equilibrium. Hence it is appropriate to use our result for parameters such that the population approaches a stable equilibrium in the absence of harvest, but possibly not for chaotic or periodic fluctuating populations. However, our results will always hold for a monotonic increasing, concave R, such as the Beverton-Holt function with parameters b_1 and b_2,

$$R(\sigma) = \frac{b_1\sigma}{1+b_2\sigma}. \tag{3.45}$$

In this case,

$$\sigma^* = \frac{1}{b_2}\left[\sqrt{\frac{\rho^2 b_1[\rho a_{21}a_{32} + a_{31}(1-\rho a_{22})]}{(1-\rho a_{11})(1-\rho a_{22})(1-\rho a_{33})}} - 1\right]. \tag{3.46}$$

Under a parameterization where $\delta < \delta_{crit}$, we show a heat map of total discounted net revenue as a function of adult and immature escapement in Fig. 3.1 and note that discounted net revenue attains its maximum when all immature biomass and σ^* adult biomass escape harvest. We also show a similar heat map, for the case where $\delta > \delta_{crit}$ and $a_{31}R(\sigma^*)/(1-a_{11}) < (1-a_{33})\sigma^*$ (see Fig. 3.2).

If $\delta > \delta_{crit}$ and $a_{31}R(\sigma^*)/(1-a_{11}) \geq (1-a_{33})\sigma^*$,

$$\hat{\sigma}^* = \frac{1}{b_2}\left[\sqrt{\frac{\rho^2 b_1[a_{21}+a_{31}]}{(1-\rho a_{11})(1-\rho a_{33})}} - 1\right]. \tag{3.47}$$

To confirm that our above analysis is in fact producing the best constant escapement policy, we compared our analytic solutions to the best escapement strategies found via numerical optimization (see online supplementary information).

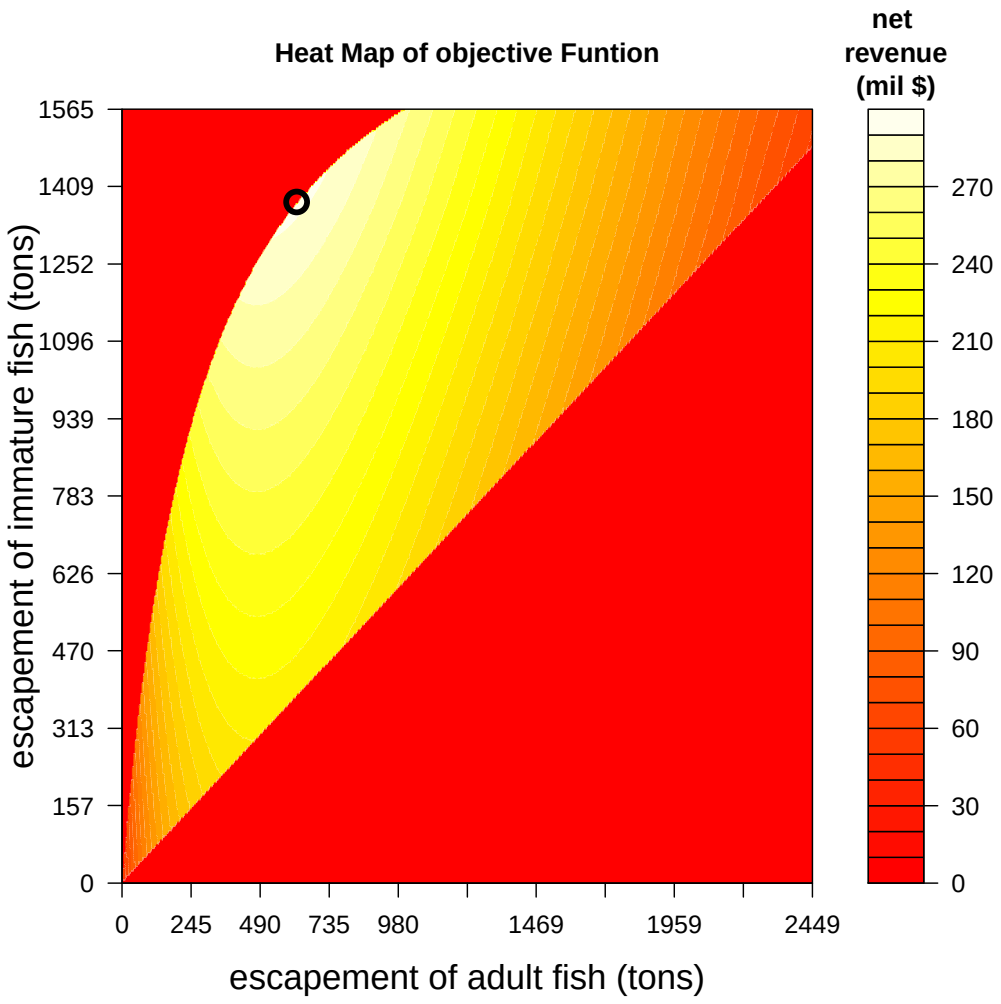

Figure 3.1: A heat map of net revenue over a grid of adult and immature fish escapement values, for a set of parameters where $\delta < \delta_{crit}$. The black circle corresponds to the optimal solution from the bioeconomic model, letting σ^* adult fish escape and leaving all immature fish in the fishery. The discounted net revenue for inadmissible strategies is set to zero (i.e. for adult/immature escapement greater than equilibrium adult/immature biomass). Parameters are $a_{32} = 1.4, a_{21} = 1.5, a_{11} = 0, a_{22} = 0.05, a_{33} = 0.1, b_1 = 4.41, b_2 = 0.000344, \delta = 0.05$. Optimal escapement and harvest of adults is $\sigma^* = 619.3$ and $h^* = 1,402.2$, respectively.

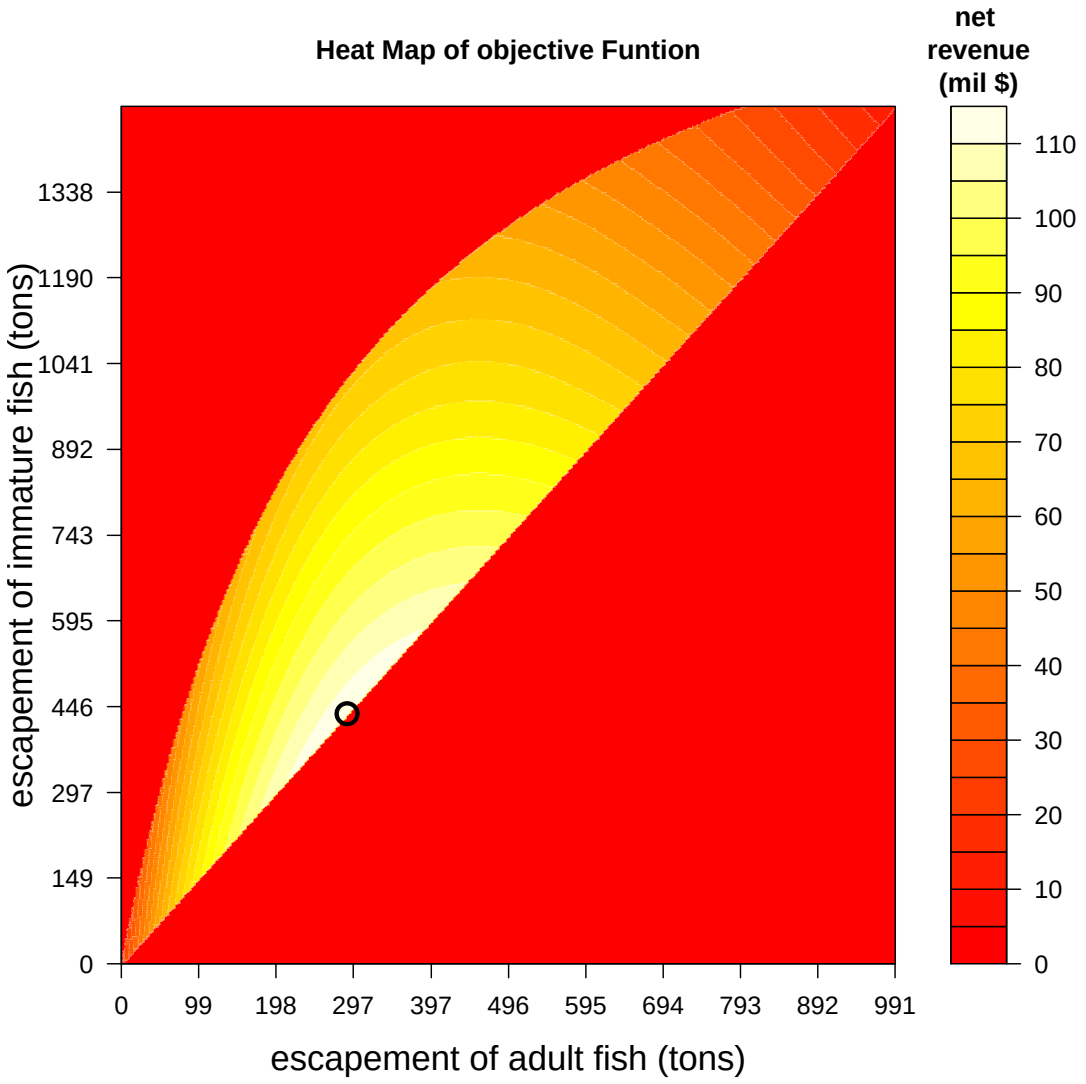

Figure 3.2: A heat map of net revenue over a grid of adult and immature fish escapement values, for a set of parameters where $\delta > \delta_{crit}$. The black circle corresponds to the optimal solution from the bioeconomic model, letting s^* immature fish escape and leaving all adult fish in the fishery. The discounted net revenue for inadmissible strategies is set to zero (i.e. for adult/immature escapement greater than equilibrium adult/immature biomass). Parameters are $a_{32} = 0.6, a_{21} = 1.5, a_{11} = 0, a_{22} = 0.05, a_{33} = 0.1, b_1 = 4.41, b_2 = 0.000344, \delta = 0.05$. Optimal escapement and harvest of immatures is $s^* = 433.7$ and $\eta^* = 546.9$, respectively.

3.4 Stochastic model and analysis

In simple one dimensional bioeconomic models, constant escapement policies can be optimal even when the biomass dynamics are stochastic. In this section, we explore these policies for structured populations. To simplify the analysis we consider two cases, one where only adult fish are harvested and the other where only immatures are harvested, both at price p (which we justify after analyzing the stochastic models). We show that environmental stochasticity affects optimal harvest in the two stage classes differently. Within each of these cases we first consider the age structured case with $a_{31} = a_{11} = a_{22} = a_{33} = 0$, and for the case of adult harvest extend the analysis to models closer to (3.1).

3.4.1 When harvesting only adults

Consider a simplified age structured model where adults die after spawning and only adult fish are harvested.

$$\begin{aligned} B_{1,t+1} &= z_{1,t+1} R(B_{3,t} - h_t) \\ B_{2,t+1} &= z_{2,t+1} a_{21} B_{1,t} \\ B_{3,t+1} &= z_{3,t+1} a_{32} B_{2,t}, \end{aligned} \tag{3.48}$$

The random variables $z_{i,t}$ are chosen such that the sequences $\{z_{i,t}\}_{t\geq 1}$ are each independently and identically distributed on a closed subset of $(0, \infty)$ with $\mathbb{E}[z_{i,t}] = 1$, in such a way that $z_{i,t}$ and $z_{j,t+m}$ are independent for all $i, j \in \{1, 2, 3\}$ and $m > 0$. In other words, we are allowing for correlation between age classes, but no temporal autocorrelation. For example, one possibility for modeling the noise is

$$z_{i,t} = \tilde{z}_t + \epsilon_{i,t}, \tag{3.49}$$

where the sequences $\{\tilde{z}_t\}_{t\geq 1}$ and $\{\epsilon_{i,t}\}_{t\geq 1}$, for each $i \in \{1,2,3\}$, are independently and identically distributed on a subset of $(0,\infty)$, with $\mathbb{E}[\tilde{z}_t] = q$, and $\mathbb{E}[\epsilon_{i,t}] = 1-q$, where $0 \leq q \leq 1$. When $q = 0$, the age classes experience independent random fluctuations. When $q = 1$, the noise is perfectly correlated between age classes.

Lastly we assume that the population is "self-sustaining" at the optimal escapement level. For example, in the case where $a_{31} = a_{11} = a_{22} = a_{33} = 0$, σ^* self-sustaining means that $z_1 z_2 z_3 a_{32} a_{21} R(\sigma^*) \geq \sigma^*$, where z_i is the lowest value $z_{i,t}$ can attain. This assumption is standard in one dimensional bioeconomic models (Clark, 2010) because it guarantees, $B_{3,t} - \sigma_t > 0$, when the system is in stationary distribution and allows for solutions achieved through stochastic dynamic programming arguments.

Because juvenile and immature fish always grow or die, and mature fish die after spawning, equations (3.48) yield three independent cohorts. Therefore, it suffices to find the optimal equilibrium escapement for a single cohort, only tracking the population in the harvested age class. Without loss of generality, consider the cohort, that is initially in the adult age class. The cohort's dynamics are given by

$$\begin{aligned} x_{\tau+1} &= \zeta_{\tau+1} a_{21} a_{32} R(x_\tau - h_\tau), \\ x_0 &= B_{3,0} \end{aligned} \tag{3.50}$$

where $x_\tau = B_{3,3\tau}$ is the adult biomass in the τth generation and $\zeta_{\tau+1} = z_{3,3\tau+3} z_{2,3\tau+2} z_{1,3\tau+1}$. The escapement policy that optimizes

$$\mathbb{E}\left\{\sum_{\tau=0}^{\infty}\rho^{3\tau}ph_{3\tau}\right\}. \tag{3.51}$$

is

$$R'(\sigma_t)=\frac{(1+\delta)^3}{a_{32}a_{21}}, \tag{3.52}$$

since this formulation satisfies the one dimensional optimization problem with fixed per unit cost and concave positive recruitment in (Reed, 1974). Note that the optimal escapement is the same as in (3.22) when substituting $a_{31}=a_{11}=a_{22}=a_{33}=0$.

Now consider the full size structured model, but again assume fishing can only occur in the adult size class. The model for adult harvest is

$$\begin{aligned}
B_{1,t+1}&=z_{1,t+1}[R(\sigma_t)+a_{11}B_{1,t}]\\
B_{2,t+1}&=z_{2,t+1}[a_{21}B_{1,t}+a_{22}B_{2,t}]\\
B_{3,t+1}&=z_{3,t+1}[a_{31}B_{1,t}+a_{32}B_{2,t}+a_{33}\sigma_t].
\end{aligned} \tag{3.53}$$

With $z_{i,t}$ as in (3.48). First we maximize expected discounted net revenue over a fixed time horizon T,

$$\mathbb{E}\left\{\sum_{t=0}^{T}\rho^{t}ph_t\right\}, \tag{3.54}$$

and then let $T\to\infty$. We proceed with a calculation similar to the one in section 7.3 of (Clark, 2010), but extend it to our three dimensional framework. Define the value function

$$V(B_t) = \max_{\sigma_t}\{p(B_{3,t} - \sigma_t) + \rho\mathbb{E}\{V(B_{t+1})\}\}. \tag{3.55}$$

At the final time it is clearly optimal to harvest everything. Hence, $\sigma_T^* = 0$, yielding

$$V(B_T) = pB_{3,T}. \tag{3.56}$$

Therefore,

$$\begin{aligned} V(B_{T-1}) &= \max_{\sigma_{T-1}}\{p(B_{3,T-1} - \sigma_{T-1}) + \rho\mathbb{E}\{pB_{3,T}\}\} \\ &= \max_{\sigma_{T-1}}\{p(B_{3,T-1} - \sigma_{T-1}) + \rho\mathbb{E}\{pz_{3,T}[a_{31}B_{1,T-1} + a_{32}B_{2,T-1} + a_{33}\sigma_{T-1}]\}\}. \end{aligned} \tag{3.57}$$

Since $a_{33} < 1$, and $B_{i,T-1}$ is known for all $i \in \{1, 2, 3\}$, $\sigma_{T-1}^* = 0$, meaning

$$V(B_{T-1}) = p(B_{3,T-1} + \rho[a_{31}B_{1,T-1} + a_{32}B_{2,T-1}]). \tag{3.58}$$

To calculate σ_{T-2}^*, we substitute $V(B_{T-1})$, into the formula for $V(B_{T-2})$ to get

$$\begin{aligned} V(B_{T-2}) = \max_{\sigma_{T-2}}\{&p(B_{3,T-2} - \sigma_{T-2}) + \rho p\mathbb{E}\{ \\ &z_{3,T-1}[a_{31}B_{1,T-2} + a_{32}B_{2,T-2} + a_{33}\sigma_{T-2}] - \sigma_{T-1}^* + \rho\mathbb{E}\{ \\ &a_{31}z_{1,T-1}[R(\sigma_{T-2}) + a_{11}B_{1,T-2}] \\ &+ a_{32}z_{2,T-1}[a_{21}B_{1,T-2} + a_{22}B_{2,T-2}]\}\}\}. \end{aligned} \tag{3.59}$$

Define

$$w_{T-2}(\sigma_{T-2}) = (\rho a_{33} - 1)\sigma_{T-2} + \rho^2 a_{31} R(\sigma_{T-2}). \tag{3.60}$$

Since $B_{i,T-2}$, for all i, are constants, the σ_{T-2} that maximizes w_{T-2} also maximizes the argument of (3.59), and hence σ^*_{T-2} is the solution to

$$R'(\sigma^*_{T-2}) = \frac{1 - \rho a_{33}}{\rho^2 a_{31}}. \tag{3.61}$$

As we proceed backwards in time, to calculate the optimal escapement strategy at time $T - n$, σ^*_{T-n}, using the methods above, a pattern emerges for $w_{T-n}(\sigma_{T-n})$. That is, for $n \geq 3$,

$$\begin{aligned} w_{T-n}(\sigma_{T-n}) = &- \sigma_{T-n} + \rho a_{33}\sigma_{T-n} + a_{31} R(\sigma_{T-n}) \sum_{j=2}^{n} \rho^j a_{11}^{j-2} \\ &+ a_{32} a_{21} R(\sigma_{T-n}) \sum_{j=3}^{n} \sum_{i=0}^{j-3} \rho^j a_{22}^i a_{11}^{j-i-3}. \end{aligned} \tag{3.62}$$

Therefore, as $T \to \infty$ and $n \to \infty$, with $n < T$, we have

$$w(\sigma) = - \sigma + \rho a_{33}\sigma + \frac{\rho^2 a_{31}}{1 - a_{11}\rho} R(\sigma) + \frac{\rho^3 a_{32} a_{21}}{(1 - \rho a_{22})(1 - \rho a_{11})} R(\sigma), \tag{3.63}$$

which means that at a stationary distribution the optimal escapement strategy is given by

$$R'(\sigma) = \frac{(1 - \rho a_{33})(1 - \rho a_{22})(1 - \rho a_{11})}{\rho^2 a_{31}(1 - \rho a_{22}) + \rho^3 a_{32} a_{21}}, \tag{3.64}$$

the same as in our deterministic analysis.

3.4.2 When harvesting immatures

Now consider the second model, where only immatures are harvested.

$$\begin{aligned} B_{1,t+1} &= z_{1,t+1}R(B_{3,t}) \\ B_{2,t+1} &= z_{2,t+1}a_{21}B_{1,t} \\ B_{3,t+1} &= z_{3,t+1}a_{32}(B_{2,t} - \eta_t). \end{aligned} \tag{3.65}$$

In this case the single cohort dynamics are given by

$$\begin{aligned} y_{\tau+1} &= \xi_{\tau+1}a_{21}R(\nu_{\tau+1}a_{32}[y_\tau - \eta_\tau]), \\ y_0 &= B_{2,0} \end{aligned} \tag{3.66}$$

where $y_\tau = B_{2,3\tau}$ is the immature biomass in the τth generation of a cohort which started as immatures, $\xi_{\tau+1} = z_{2,3\tau+3}z_{1,3\tau+2}$, and $\nu_{\tau+1} = z_{3,3\tau+1}$. We wish to find the escapement that optimizes

$$\mathbb{E}\left\{\sum_{\tau=0}^{T}\rho^{3\tau}p\eta_{3\tau}\right\}. \tag{3.67}$$

Since R is a function of a random variable, we can no longer directly apply the theorem from (Reed, 1979), but we can use a similar stochastic dynamic programming argument as we did for to derive the optimal escapement policy. Define the value function,

$$V(y_\tau) = \max_{s_\tau}\{p(y_\tau - s_\tau) + \rho^3\mathbb{E}\left[V(y_{\tau+1})\right]\}. \tag{3.68}$$

Iterating backwards, we find that $s_T^* = 0$, and

$$V(y_{T-1}) = \max_{s_{T-1}} \{p(y_{T-1} - s_{T-1}) + \rho^3 \mathbb{E}\left[p\xi_T a_{21} R(\nu_T a_{32} s_{T-1})\right]\}. \tag{3.69}$$

Since y_{T-1} is assumed to be known, finding s^*_{T-1} is equivalent to finding the s that maximizes

$$w(s) = -s + \rho^3 a_{21} \mathbb{E}\left[R(\nu_{\tau+1} a_{32} s)\right]. \tag{3.70}$$

Therefore the optimal s is the solution to

$$\mathbb{E}\left[\nu_{\tau+1} R'(\nu_{\tau+1} a_{32} s)\right] = \frac{(1+\delta)^3}{a_{32} a_{21}}. \tag{3.71}$$

Note that for earlier τ the form of w is the same and hence if we take T to infinity, the solution to (3.71) is the optimal stationary immature escapement. For a logistic recruitment function, this equation has a closed form solution, since

$$\mathbb{E}\left[\nu_{\tau+1} R'(\nu_{\tau+1} a_{32} s)\right] = r - \frac{2r a_{32} s_t}{k} \mathbb{E}\left[\nu^2_{\tau+1}\right], \tag{3.72}$$

which means the optimal escapement is

$$s_t = \left[\frac{k}{2r a_{32}}\right] \left[r - \frac{(1+\delta)^3}{a_{32} a_{21}}\right] \left[\frac{1}{1 + \mathrm{var}(\nu_{\tau+1})}\right]. \tag{3.73}$$

which is just $1/(1 + \mathrm{var}[z_{3,t}])$ times the optimal escapement policy for a deterministic model with logistic recruitment. This means, that when recruitment and survival vary randomly over time, if a manager chooses to fish immature biomass,

he should fish more aggressively than in the deterministic case, because the non-linear recruitment function lessens the benefit from good years. However, if the manager harvests adults, he should do so as if the system is deterministic.

In order to verify these predictions, we simulated 20 million realizations of this system with the environmental noise distributed as a discrete probability distribution, $z_t = 0.8$ with probability $5/7$ and $z_t = 1.5$ with probability $2/7$, under eight immature escapement strategies including the analytic stochastic optimal escapement rule (3.73) and the deterministic optimal escapement rule (see figure 3.3). Note that the calculations require the population to be self sustaining at the optimal escapement value, such that $B_{2,t} - s_t^* \geq 0$ for all t, at stationary distribution. When this assumption is violated, the optimal escapement policy is still lower than in the deterministic setting, however $1/(1 + \text{var}(z_t))$ may be an overcorrection. See figure 3.4 for an example where three "bad years" can cause less immature biomass to return to the immature phase than what initially escaped three years prior, and notice that the general concept that you fish more aggressively in the stochastic model, with logistic recruitment, is still true.

3.4.3 The effect of the recruitment function

The logistic recruitment function allowed for a closed form analytic solution to equation (3.71). However, there is no analytically tractable solution to (3.71) for most density dependent recruitment functions. We would like to know if the result that a manager should fish immatures more aggressively under environmental stochasticity is general for all density dependent recruitment functions.

Let s^* be the optimal escapement of immature fish if there is no stochas-

ticity. In this case equilibrium spawner biomass is $\sigma^* = a_{32}s^*$. We note that if

$$\mathbb{E}\left[\nu_{\tau+1}R'(\nu_{\tau+1}\sigma^*)\right] > \frac{(1+\delta)^3}{a_{32}a_{21}}, \tag{3.74}$$

then the expected biological growth rate is higher than the discount rate and one should therefore leave more fish in the ocean (i.e. increase escapement, higher than s^*). If

$$\mathbb{E}\left[\nu_{\tau+1}R'(\nu_{\tau+1}\sigma^*)\right] < \frac{(1+\delta)^3}{a_{32}a_{21}}, \tag{3.75}$$

then escapement should be decreased under environmental stochasticity. Define

$$f(\nu) = \nu R'(\nu\sigma^*). \tag{3.76}$$

By Jensen's Inequality, if f is strictly convex on the support of ν,

$$\mathbb{E}\left[f(\nu)\right] > f(\mathbb{E}\left[\nu\right]) = f(1) = \frac{(1+\delta)^3}{a_{32}a_{21}}. \tag{3.77}$$

Similarly if f is strictly concave on the support of ν

$$\mathbb{E}\left[f(\nu)\right] < f(\mathbb{E}\left[\nu\right]) = f(1) = \frac{(1+\delta)^3}{a_{32}a_{21}}. \tag{3.78}$$

This means that if $f''(\nu) > 0$, for all ν, equation (3.74) is satisfied and it is more profitable to increase escapement. If $f''(\nu) < 0$, for all ν, (3.75) is satisfied and it is more profitable to decrease escapement. Noting that

$$f''(\nu) = 2\sigma^* R''(\nu\sigma^*) + (\sigma^*)^2 \nu R'''(\nu\sigma^*), \tag{3.79}$$

it is possible to calculate when fishing should be more or less aggressive for specific recruitment functions even when such functions do not allow for tractable solutions to equation (3.71).

For logistic recruitment, (3.42), we note that $f''(\nu) < 0$ for all $\nu > 0$ and $\sigma^* > 0$, meaning it is more profitable to decrease the escapement of immatures. This agrees with our analytic optimal escapement rule (3.73).

More aggressive fishing than in the deterministic case is also optimal if recruitment follows a Ricker curve,

$$R(\sigma) = b_1 \sigma e^{-b_2 \sigma}, \tag{3.80}$$

with $b_2 > 0$. In this case $f''(1) < 0$ for all $\sigma^* < 1/b_2$. Since for Ricker recruitment $R'(\sigma) < 0$ for all $\sigma > 1/b_2$, by equation (3.22), σ^* will always be less than $1/b_2$. Therefore, as long as the support of ν does not contain values large enough that $\nu\sigma^* > 1/b_2$, it will be more profitable to decrease escapement. It should be noted that since the Ricker function is not concave on it's entire domain, our analysis is not guaranteed to hold in this case. However, we simulated expected discounted net revenue when harvesting immatures in a stochastic fishery with a Ricker spawner-recruitment relationship, and the example agrees with our result (Fig. 3.5).

Similarly it can be shown that for the monotone Recruitment function $R(\sigma) = b_1 \log(1 + b_2\sigma)$ that it is also always profitable to decrease escapement. However, this is not true for all monotone recruitment functions. For Beverton-

Holt recruitment, (3.45), both more aggressive and more conservative fishing can be optimal depending on the parameters. In this case, $f''(\nu) > 0$ for all ν if $b_2\sigma^* \min(\nu) > 2$, and $f''(\nu) < 0$ for all ν if $b_2\sigma^* \max(\nu) < 2$. Substituting in

$$\sigma^* = \frac{1}{b_2}\left[\sqrt{\rho^3 b_1 a_{21} a_{32}} - 1\right], \tag{3.81}$$

means that it is more profitable to increase immature escapement if $\sqrt{\rho^3 b_1 a_{21} a_{32}} > 1 + 2/\min(\nu)$ and decrease escapement if $\sqrt{\rho^3 b_1 a_{21} a_{32}} < 1 + 2/\max(\nu)$.

The above example highlights how optimal immature escapement, under environmental stochasticity depends on the third derivative of R. Since the second derivative of R will be negative for all compensatory and over-compensatory recruitment functions near σ^*, it is always more profitable to fish more aggressively when R''' is negative. However, increasing escapement can be more profitable if $R'''(\sigma^*)$ is positive, especially if σ^* is large.

Table 3.1: The effect of environmental stochasticity on the optimal escapement of immature fish for different spawner-recruitment relationships when the variance of the environmental noise is small.

Recruitment Function	**Functional form**	**parameter constraints**	**Effect of stochasticity on immature escapement**
Discrete Logistic	$R(\sigma) = b_1\sigma(1 - \sigma/b_2)$	$b_1 > 0, b_2 > 0$	decrease escapement
Ricker	$R(\sigma) = b_1\sigma e^{-b_2\sigma}$	$b_1 > 0, b_2 > 0$	decrease escapement
Beverton-Holt	$R(\sigma) = b_1\sigma/(1 + b_2\sigma)$	$b_1 > 0, b_2 > 0$	decrease escapement if $\sigma^* < 2/b_2$, increase escapement if $\sigma^* > 2/b_2$
Log	$R(\sigma) = b_1 \log(1 + b_2\sigma)$	$b_1 > 0, b_2 > 0$	decrease escapement

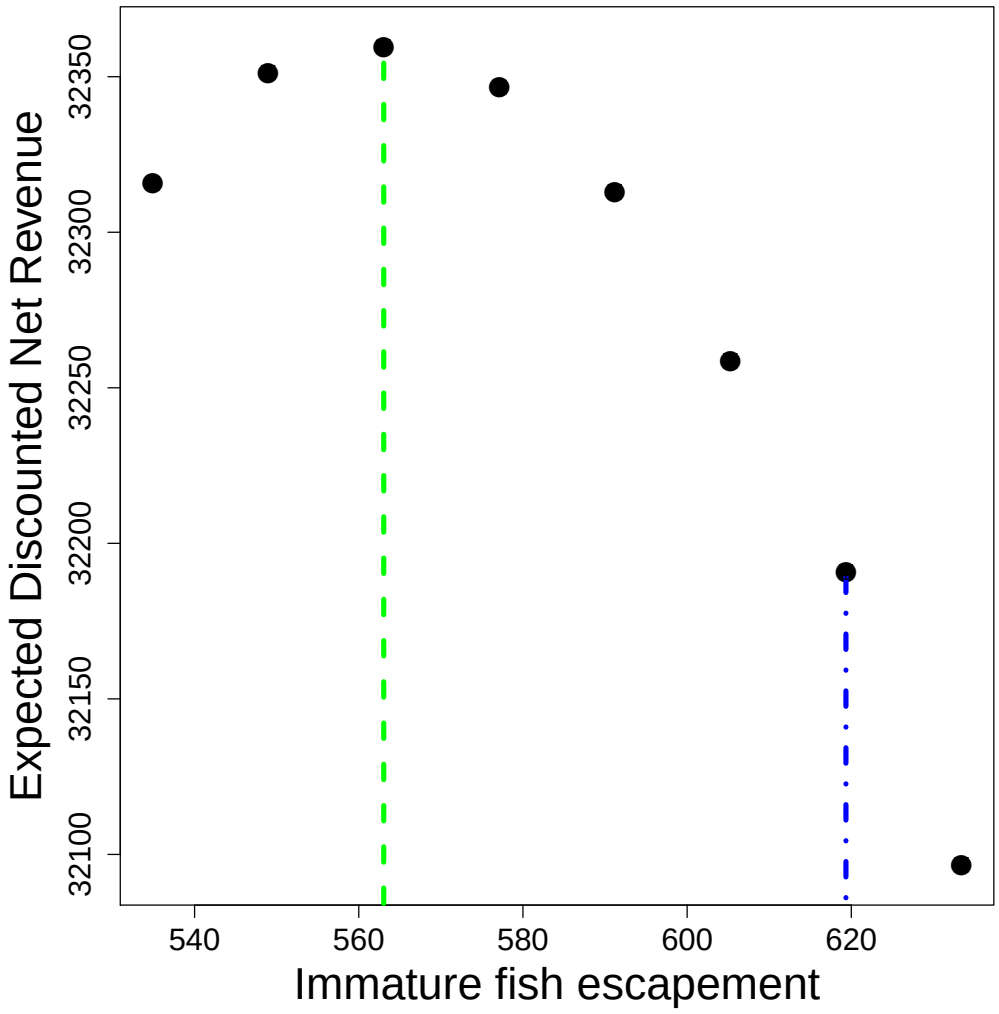

Figure 3.3: Expected net revenue for eight immature fish escapement strategies, averaged over ten million simulations (confidence intervals are negligible due to the large sample size). The green dashed line is the analytic "variance corrected" optimal escapement strategy in the stochastic logistic recruitment model (563.0) and the blue line corresponds to the optimal escapement strategy for the corresponding deterministic model (619.3). The parameters are $a_{32} = 0.83, a_{21} = 2, r = 1.65, K = 2000, p = 5, T = 55, \delta = 0.1$ and $z_t = 0.8$ with probability 0.7143 and $z_t = 1.5$ with probability 0.2857.

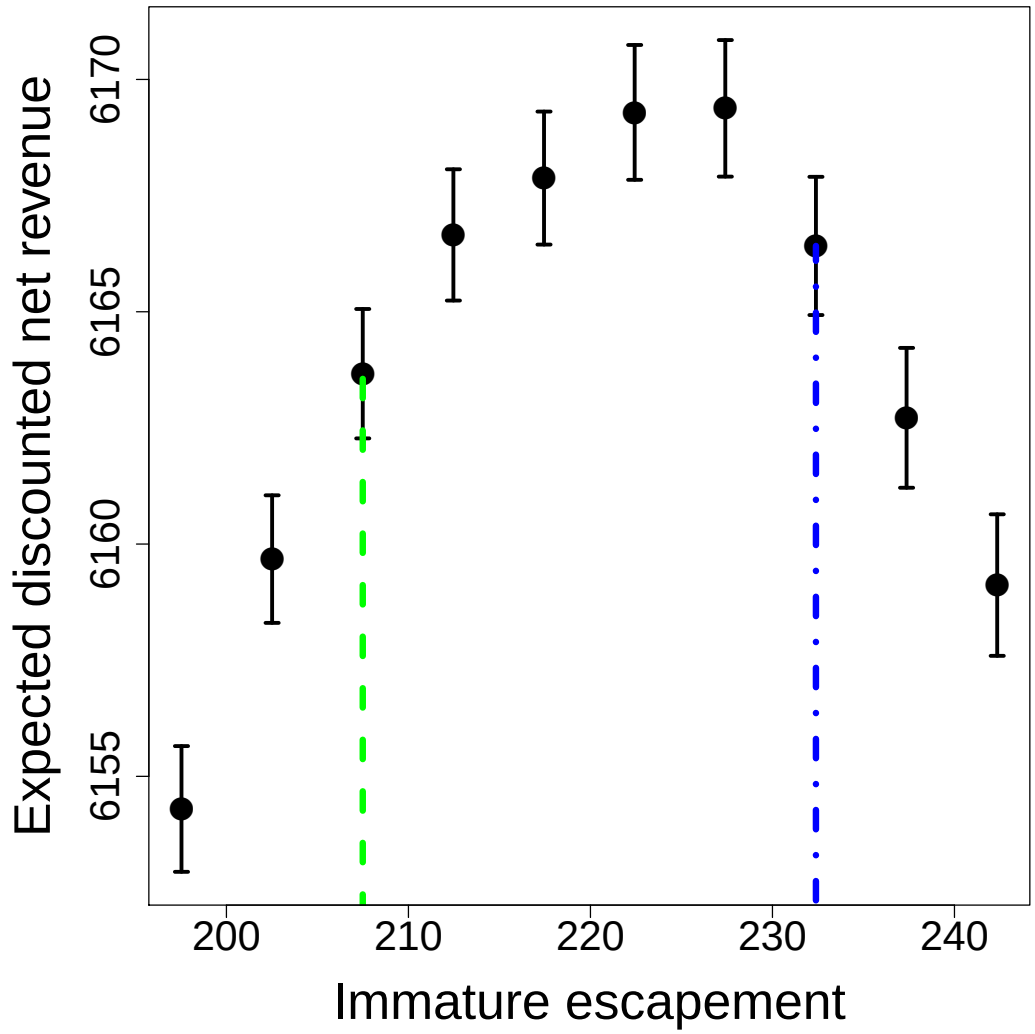

Figure 3.4: Expected net revenue for eight immature fish escapement strategies, averaged over ten million simulations with 95 percent confidence intervals. $z_{1,t} = z_{2,t} = z_{3,t}$, with $z_{1,t}$ distributed uniformly on $(0.4, 1.6)$. The green dashed line is the "variance corrected" optimal escapement strategy in the stochastic logistic recruitment model and the blue line corresponds to the optimal escapement strategy for the corresponding deterministic model. The parameters are $a_{32} = 0.9, a_{21} = 1.05, a_{11} = a_{22} = a_{33} = 0, r = 1.5, K = 2000, p = 5, T = 55, \delta = 0.1$. Note that in this case the assumptions used to derive the optimal escapement strategy do not hold because $B_{2,t} - s_t^* \geq 0$ requirement is not satisfied for all t, since $0.4^2 a_{21} R(0.4 a_{32} s^*) < s^*$ (meaning a series of bad years can send the stock below the calculated optimal escapement level). However, the general concept that you fish more aggressively in the stochastic model is still true in this example.

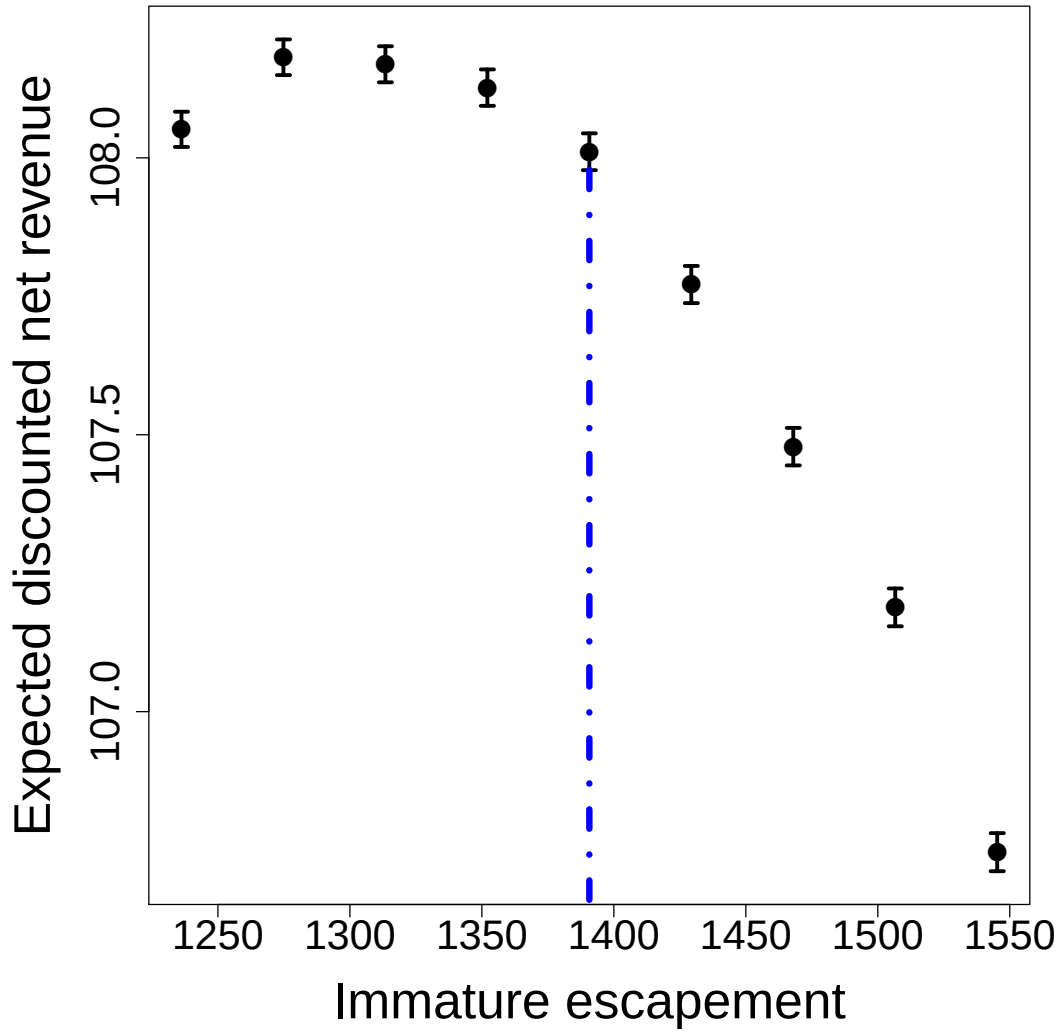

Figure 3.5: Expected discounted net revenue for 9 immature escapements for a stochastic fishery with Ricker recruitment with 95 % confidence intervals, averaged over one million simulations. The blue dashed line is the optimal escapement strategy for the corresponding deterministic model (1390.7), calculated by solving (3.22) numerically using an implementation of the Newton-Raphson method in R. The parameters are $a_{32} = 1.2, a_{21} = 1.1, b_1 = 2, b_2 = 0.0002, p_2 = 3.43, p_3 = 1.66, T = 70, \delta = 0.08$ and $z_t = 0.8$ with probability 5/7 and $z_t = 1.5$ with probability 2/7.

3.4.4 Justification of single stage harvest

In the stochastic case, we only calculated the optimal escapement strategy assuming exclusive harvest of either adults or immatures. This was a mathematical simplification. However, exclusive harvest will be optimal in the stochastic system in some circumstances.

Consider model (3.53), with the addition of immature harvest and stage specific pricing, as in the deterministic optimization problem (p_2 and p_3, the price per unit biomass of immatures and adults respectively). Below, we prove that under environmental stochasticity, it is less profitable, in expectation, to increase immature harvest from zero, given any self-sustaining adult escapement strategy, as long as the condition for exclusive adult harvest in the deterministic model is met.

Proposition 3.2. *When letting σ units of adult biomass escape harvest, assuming σ is self-sustaining, if $\delta < \delta_{crit}$, then in comparison to harvesting $h_t = B_{3,t} - \sigma$ adults and $\eta_t = 0$ immatures, harvesting an additional small amount of immature biomass $\eta_t > 0$, decreases expected discounted net revenue.*

Proof. Assume a self sustaining adult escapement strategy, σ, and let J be expected net revenue of harvesting $B_{2,t} - s$ adult biomass and η_t immature biomass, for each year t,

$$J = \mathbb{E}\left\{\sum_{t=0}^{\infty} \rho^t (p_2\eta_t + p_2[B_{3,t} - \sigma])\right\}. \tag{3.82}$$

We show that if $\delta < \delta_{crit}$, then $\partial J/\partial \eta_\tau < 0$, for all η_τ such that σ adult escapement is self-sustaining.

$$\begin{aligned}\frac{\partial J}{\partial \eta_\tau} &= \mathbb{E}\left\{\rho^\tau p_2 - \rho^{\tau+1}\eta_\tau z_{3,\tau+1}\left(1+\sum_{i=1}^{\infty}\prod_{j=0}^{i-1} z_{2,\tau-j}\rho^i a_{22}^i\right)\right\} \\ &= \rho^\tau\left(p_2 - \frac{\rho p_3 a_{32}}{1-\rho a_{22}}\right).\end{aligned} \tag{3.83}$$

Which is less than zero if $\delta < \delta_{crit}$, as defined in equation (3.29). □

Consider (3.65) with the addition of adult harvest and stage specific pricing. In this case, a manager should not harvest any adults for small fluctuations in adult biomass above optimal adult escapement (the expected adult biomass that results from letting $a_{32}s^*$ immature biomass escape). However, when fluctuations are large, in good years, there is potentially a benefit to harvesting some excess adult biomass prior to recruitment. This can be summarized as a proposition.

Proposition 3.3. *When letting s units of immature biomass escape harvest, assuming s is self-sustaining, if $\rho^2 p_2 a_{21} R'(\max(z_{3,t})a_{32}s) > p_3$, then in comparison to harvesting $\eta_t = B_{2,t} - s$ immatures and $h_t = 0$ adults, harvesting any additional adults $h_t > 0$, decreases expected discounted net revenue.*

Proof. Assume an immature escapement strategy, s, is deployed and let J be expected net revenue,

$$J = \mathbb{E}\left\{\sum_{t=0}^{\infty}\rho^t(p_3 h_t + p_2[B_{2,t} - s])\right\}. \tag{3.84}$$

We show that if $\rho^2 p_2 a_{21} R'(\max(z_{3,t})a_{32}s) > p_3$, then $\partial J/\partial h_\tau < 0$, at $h_\tau = 0$, for any arbitrary time τ.

$$\begin{aligned}\frac{\partial J}{\partial h_\tau} &= \mathbb{E}\left\{\rho^\tau p_3 - \rho^{\tau+2} p_2 z_{2,\tau+2} z_{1,\tau+1} a_{21} R'(z_{3,\tau} a_{32} s_\tau - h_\tau)\right\} \\ &\leq \rho^\tau [p_3 - \rho^2 p_2 a_{21} R'(\max(z_{3,t}) a_{32} s_\tau - h_\tau)].\end{aligned} \tag{3.85}$$

The inequality is guaranteed by the assumption that R is concave. Plugging in $h_\tau = 0$ yields the desired result.

□

3.5 Hard clam example

Historically, the hard clam fishery has been one of the most lucrative fisheries in New York State and the largest shellfish fishery on the east coast of North America (Bricelj et al., 1980). We use a snap-shot of this fishery circa 1980 as an example for our model. In New York, the clams are sold in three common varieties: littlenecks (width $<$ 36.5mm), cherrystones (width $<$ 41.3mm) and chowders (width $>$ 41.3mm) (Bricelj et al., 1980). As the clams grow, their flesh becomes tough and less desirable. Although smaller clams command the highest price, it is illegal to harvest clams with a width less than 25.4mm in the United States (Bricelj et al., 1980). We classify the clams that are too small to be legally harvested as juveniles, littleneck clams as immatures and both cherrystones and chowders as adults. Clams with a width less than 25mm do not typically contribute to reproduction (Bricelj et al., 1980). While littleneck clams can reproduce, their average fecundity is only about one third of cherrystones and chowders and hence we ignore it as a mathematical simplification. On average it takes juveniles two years to grow larger than 25.4mm, and another two years to become cherrystones (Kennish and Loveland, 1980). The probability a juvenile survives is 0.16 (Connell, 1983) and in

the absence of harvest, immature and adult survival is 0.91 (Carriker, 1961). The respective weights of the three sizes of clam were calculated from their shell length as reported by Anderson et al. (1978) using the relationship weight[g] = (0.671 × length[cm])^3 (Haskin, 1954), yielding juvenile, immature and adult clam weights of 0.01, 0.13 and 0.35 lbs respectively. The above assumptions yield parameters,

$$a_{11} = (\text{survival prob.})(\text{transition prob.}) = 0.16 \times 1/2 = 0.08,$$
$$a_{21} = (\text{survival prob.})(\text{transition prob.})(\text{growth}) = 0.16 \times 1/2 \times 0.13/0.01 = 1.04,$$

with the rest calculated similarly, giving $a_{22} = 0.46, a_{32} = 1.23$, and $a_{33} = 0.91$. An Adult clam produces, on average, seven million eggs per spawning event, but the probability of larvae survival is very small, estimated at 0.00058 over five days (Carriker, 1961). Assuming larva survival continues at this rate for the ten days it takes to develop into a juvenile clam (studies reviewed in Fegley (2001) ranged from eight days to two weeks) and that recruitment follows the Beverton-Holt model, then $b_1 = 2.35$. The carrying capacity of this fishery is unknown, so we set it to be equal to the largest reported historical landing (as reported in Conrad (1982)), yielding $b_2 = 6.08 \times 10^{-5}$. On October 1, 1980 the per pound price ratio p_3/p_2 was 0.24 (Conrad, 1982). We set the discount rate to match the interest rate of a 10 year U.S. treasury note, which was $\delta = 0.1175$ (Oct. 1, 1980).

In 1980, due to high inflation, it was much more valuable to fish the immature stage class exclusively (Fig. 3.7). The sensitivity of the optimal equilibrium biomass to the parameter values is shown in Fig. 3.6. As is standard for bioeconomic models, higher discount rates lead to lower equilibrium stock biomass. Equilibrium biomass increases with a_{ij}. If a_{22} is small, only immatures are har-

vested, but for large a_{22} harvest switches to adults and stock sizes increase. As a_{31} increases, optimal harvest switches from only fishing immatures to harvesting some adults in addition to all of the immatures. This is important because it says that if the probability of transitioning from a sub-legal size clam directly into a cherrystone was underestimated, it could explain why cherrystones and chowders are harvested in practice.

Using the parameters above and a discount rate of $\delta = 0.05$ we consider adding environmental stochasticity to this example as described in (3.48), with $z_{1,t} = z_{2,t} = z_{3,t}$ and $z_{1,t}$ independently identically distributed such that $z_{1,t} = 0.8$ with probability $5/7$ and $z_{1,t} = 1.5$ with a probability $2/7$. In this case, stochasticity means the best strategy is to fish more conservatively than in the deterministic scenario (see Fig. 3.8). Based on our analytic calculation, we would expect this result because high adult survivorship, $a_{33} = 0.91$, means $\sigma^* > 2/b_2$. [1]

If stochastic fluctuations are higher for hard clam than in this hypothetical example, proposition (3.3) also suggests a possible reason for why commercial fishing operations harvest adults in practice, at least in good years.

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[1]Note we assumed $a_{33} = 0$ in our analytic calculation for immature harvest under environmental stochasticity. However, the calculation provides intuition for the case when $a_{33} > 0$.

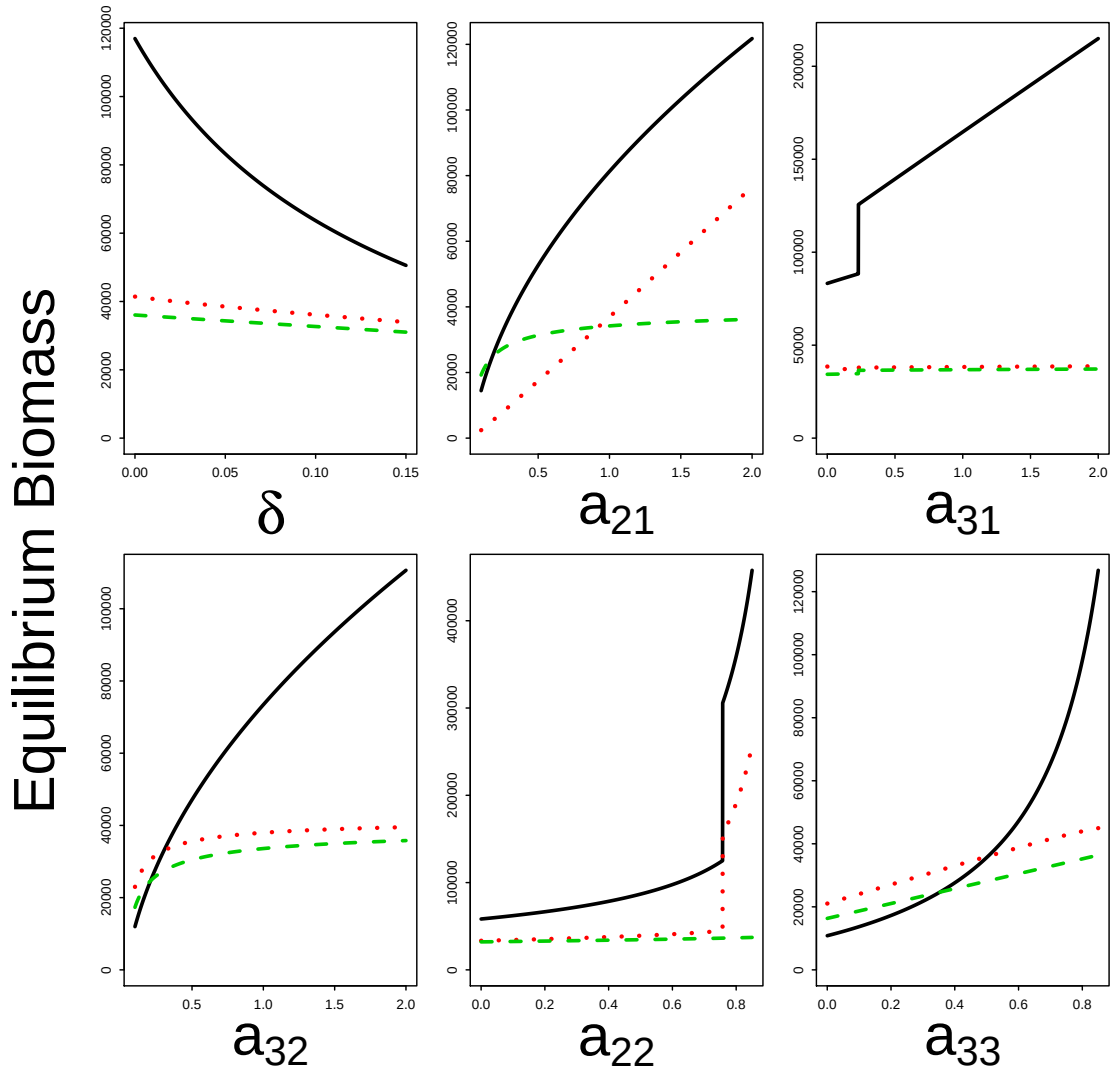

Figure 3.6: Equilibrium adult (black solid line), immature (red dotted line) and juvenile (green dashed line) biomass as a function of each parameter. Recruitment is Beverton-Holt and baseline parameter values are $a_{11} = 0.08, a_{21} = 1.04, a_{22} = 0.46, a_{32} = 1.23, a_{33} = 0.91, \delta = 0.05, p_2 = 1.01, p_3 = 0.24, b_1 = 2.3$, and $b_2 = 6.08 \times 10^{-5}$ and were chosen to match values reported in the literature for hard clam.

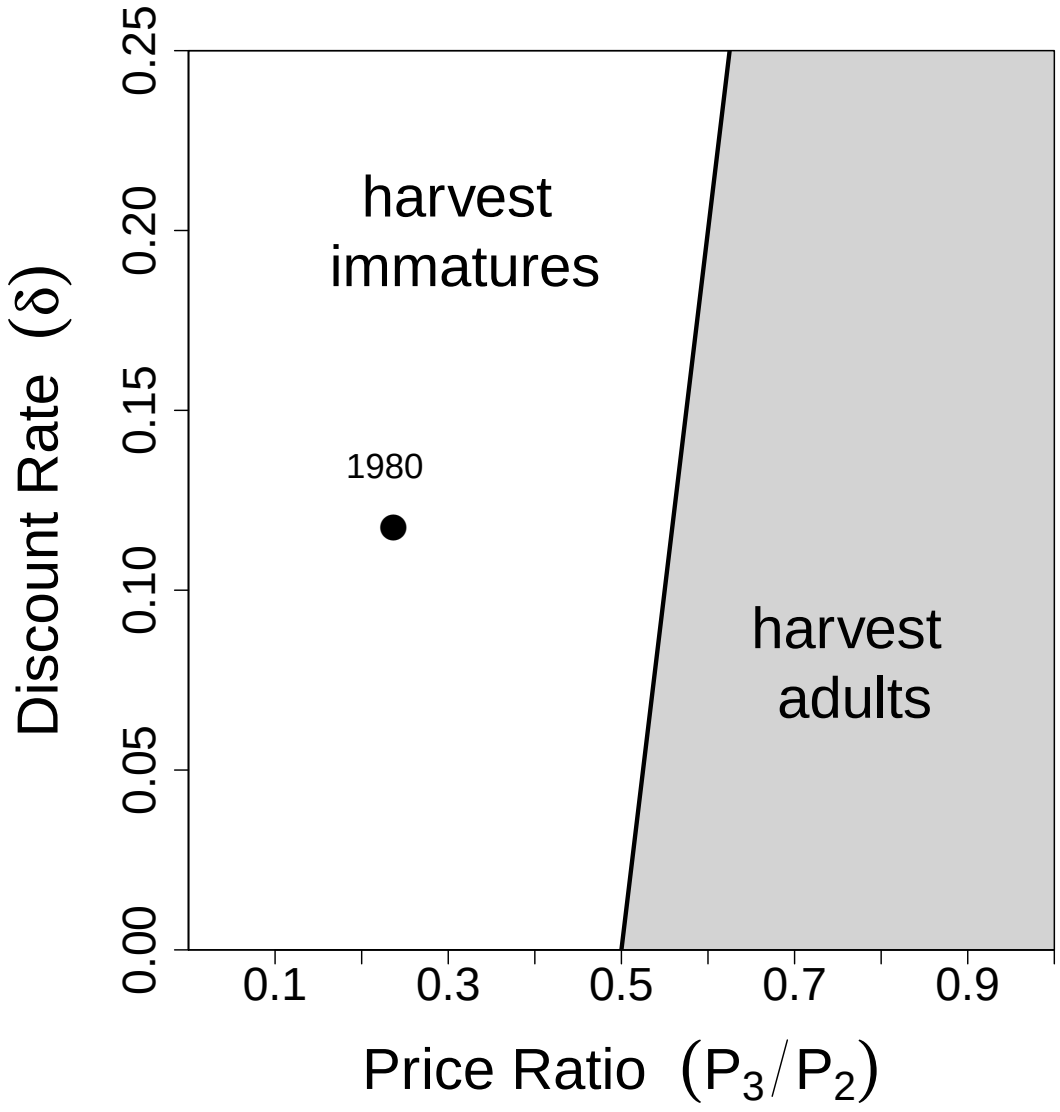

Figure 3.7: A bifurcation diagram for when it is optimal to harvest immature clams vs. adult clams, given the life history parameters for hard clam. The dividing line is the discount rate, δ_{crit}, at which it is equally profitable to harvest either stage class, as a function of the price ratio p_3/p_2. Parameters values are $a_{11} = 0.08, a_{21} = 1.12, a_{22} = 0.46, a_{32} = 1.17, a_{33} = 0.91, b_1 = 2.3, b_2 = 6.08 \times 10^{-5}$. The point labeled 1980 correspond to the price ratio from data in (Conrad, 1982) and discount rate matching the interest rate on a 10 year U.S. treasury note.

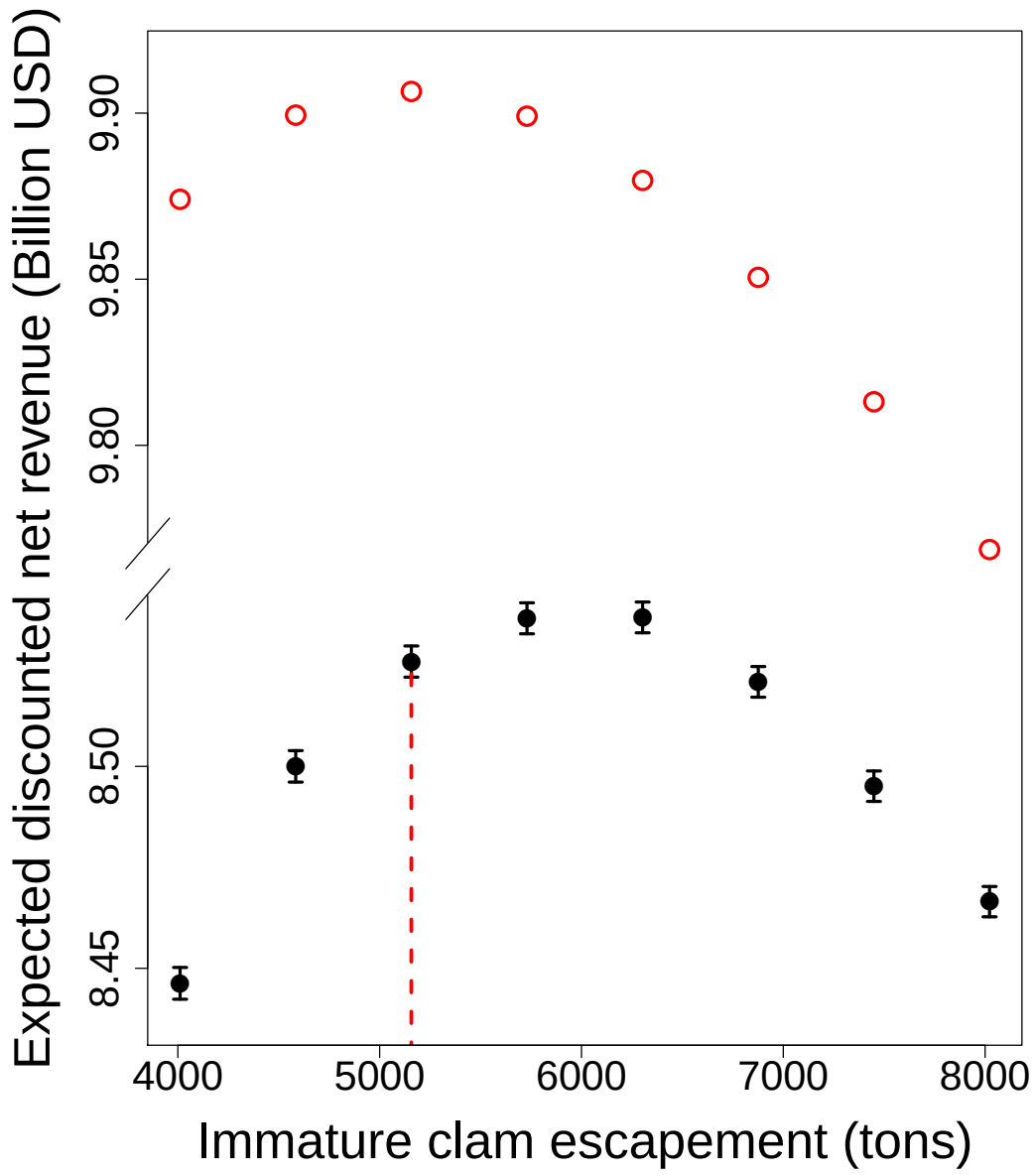

Figure 3.8: Expected discounted net revenue for hard clam escapement levels in the stochastic model (black closed circles with 95 % confidence intervals) and for the deterministic model (Red open circles). The red dashed line corresponds to the theoretical optimal escapement in the deterministic model.

3.6 Discussion

While optimal harvest strategies for age structured populations have been widely studied in the bioeconomics literature, little is known about how environmental stochasticity affects the optimal harvest of structured populations. In this paper, we developed optimal escapement rules for a stage structured fish stock, where transitions between all classes were possible (except for shrinking) and used a stochastic version of the model to extend classic theoretical results on the optimal harvest of stochastic one dimensional models (Reed, 1979) to structured populations.

Two discrete time, size structured models have been analyzed previously (Getz and Haight, 1989; Tahvonen, 2014). Some aspects of Tahvonen's model are more general than ours, including a nonlinear objective function and the possibility that all harvested stage classes can reproduce. These generalities combined with the assumption that harvest occurs after adult recruitment, can lead to the existence of cyclical interior solutions corresponding to partial harvests of both immature and adult stages. Tohoven, reveals this possibility by studying the stability of optimal harvest solutions. Since our primary goal was to study the effect of stochasticity we leave stability analysis in our deterministic setting as future direction.

However, other aspects of Tahoven's model are more restrictive, such as the assumption that individuals do not skip stages and that dynamics are deterministic. Some species can undergo short periods of rapid growth with high variability between individuals, and hence skipping stages may be common for structured populations. For example, it is possible for a large juvenile clam to transition into a cherrystone in one year (Kennish and Loveland, 1980). We have shown how

skipping stages can create an additional case where it is optimal to harvest all of the early stage and in addition partially harvest the late stage, even though it is less valuable.

For a linear objective function, as in one dimensional models (Reed, 1979), stochasticity does not affect optimal escapement, as long as the optimal escapement level is self-sustaining and the harvest of reproductive individuals occurs prior to recruitment. However, if harvest occurs during an immature stage, we showed that random fluctuations in stock dynamics can affect the optimal escapement strategy depending on the shape of the recruitment function.

In the stochastic model, we assumed the manager was either exclusively harvesting immatures or adults. Exclusive adult harvest is indeed optimal under the same condition as in the deterministic problem. However, when this condition is not met, we can only show that exclusive immature harvest is optimal for tightly bounded noise. For large fluctuations, partial harvest of adults and immatures may be optimal, and hence future analysis is required to determine the best harvest strategies.

The effect of stochasticity on optimal harvest with nonlinear utility remains an open question for stage structured fisheries. It should be possible to do similar analysis to what we have done here if the objective function is separable. For one dimensional models, Reed (1979) showed that if utility is concave, stochasticity increases optimal escapement and if utility is convex, stochasticity decreases optimal escapement. It is important to note that concave utility in Reed's one dimensional models and concave recruitment in our stage structured model, when harvesting immatures, have a diametrically opposite effect on optimal escapement if the third derivative of the recruitment function is negative. Future analysis should shine

light on the interplay between these two nonlinearities when determining optimal harvest in stochastic fisheries.

CHAPTER 4

HUMAN JUDGMENT VS. MATHEMATICAL MODELS FOR THE MANAGEMENT OF BIOLOGICAL POPULATIONS

Abstract

Despite major advances in computing, optimization and ecological modeling there has been resistance to using these techniques in the actual practice of environmental management. Mathematical models have the advantage of providing objective criteria for making environmental decisions. However, models that mis-specify key ecological processes can greatly reduce profits and sustainability. While managers using experience and judgment develop more subjective decisions, their process is not constrained by rigid mathematical assumptions and therefore can potentially be more flexible than model based policies. In this chapter we explore how well humans, using their experience and judgment, manage simulated populations and compare their management outcomes to the performance of a variety of mathematical models with varying degrees of correctness. We consider models that (1) perfectly represent the system (2) specify the system correctly but must estimate parameters in real time from the data (3) mis-specify the functional forms in the system and (4) ignore age structure. Humans on average perform much worse than the models in cases 1 - 3, but in some scenarios models can still produce worse outcomes than those resulting from human management. This highlights the possibility that active adaptive management, potentially reducing present benefits in order to learn about the system and improve future management, may improve long term objectives. In case 4, when models ignore age structure, they generated poorly performing management decisions. However, they still outperformed humans using experience and judgment 66 percent of the time.

4.1 Introduction

In the past 50 years environmental management has benefited from major advances in decision science. Theoreticians, scientists and government agencies widely agree that given appropriate budgets, adaptive management, the iterative use of system monitoring, modeling, and optimization to reduce uncertainty and improve objectives, is the best way to manage a biological population (Walters, 1986; Possingham et al., 2001; Williams, 2001; Stankey et al., 2005). While managers often do practice some components of adaptive management by collecting data and making decisions based on their expertise, with the exception of a few lucrative large scale management problems in fisheries, waterfowl and forestry (e.g. Sainsbury, 1988; Gerber et al., 2005; Moore and Conroy, 2006; Nichols et al., 2015), very few managers use dynamic modeling and optimization for environmental decision making.

One potential reason for the resistance to using mathematical modeling in management is that it's unclear how much modeling and optimization actually improve management outcomes over expert opinion. Experiments in management are in general not repeatable. That is, once a manager makes a decision based on their expertise, it is usually impossible to compare the outcome to how well an alternative decision, aided by a mathematical model, would have done.

In this chapter we take a first step towards quantifying the economic benefits of using simple dynamic models and optimization methods, rather than human intuition, to manage biological populations, by comparing the outcomes from humans and models managing simulated populations. To do this, students in multiple college classes played an online game where they managed a simulated fishery. The data from each game was saved on a server, and therefore we were able to com-

pare exactly how mathematical models would have played, compared to how the students actually played, for each unique instance of the game.

We found that mathematical models, *on average*, performed much better than humans, even when the models incorrectly specified the states of the system and the functional form of the dynamics. However, humans operating based on experience and judgment, without the aid of mathematics, sometimes made better management decisions than theoretical models when (1) population dynamics exhibited large random fluctuations in biomass due to environmental stochasticity, and (2) past data used for model fitting, generated by the user playing a short practice game, was restricted to a narrow window of population biomasses. When both (1) and (2) were satisfied, it was difficult to fit the dynamic models to the data, and poor fits led to poor management decisions.

These results emphasize the importance of techniques from active adaptive management when using modeling to make environmental decisions, otherwise risk adverse managers might prefer intuition compared to using simple mathematical models. Ultimately, because the models greatly improved management outcomes on average, but performed poorly in some scenarios, we recommend that managers use models to aid decision making but recognize that modeling will sometimes require human intervention and therefore cannot act as a replacement for expert judgment.

4.2 Methods

4.2.1 Experiments

Students played two online "games", accessed using a web browser, where they earned "points" corresponding to the profits from managing a simulated herring and pacific salmon fishery. Below we describe the experiment for the herring fishery game and then provide an explanation for how the salmon game was different.

The students played the game using their laptops during the lecture period of two courses, "Environmental Conservation" at Cornell University and "Principles of Biology" at Ithaca College, and at the "Graduate Student Science Colloquium" at Cornell University. Prior to managing each fishery, the students filled out a multiple choice survey that asked them their major, educational experience, fishing experience, and environmental management experience. See section 7.1 for a copy of the survey.

After the survey, each game showed a page of directions describing the fish stock's population dynamics. In addition, the game facilitator read a script aloud reiterating the points listed on the page. This included statements about the existence of a fishery carrying capacity, measurement error, environmental randomness out of the managers control and how their performance would be scored. See section 7.2 for a copy of the game directions. Before starting the game each student was randomly assigned a σ between 0 and 0.25. Students with high σ experienced large random variation in stock biomass unrelated to their management actions. Before playing the game the students played an 8 turn practice game. This served three purposes: (1) they developed experience with

the fishery (2) we used the data from the practice game to identify students who didn't understand the directions and (3) it provided a set of "past data" for the models and students to use as a basis for making decisions in the future.

When the user started the game, they were presented with 3 harvest data points, and the resulting biomasses from the deterministic version of the model underlying the simulated population dynamics, to give them some context of the range of harvest values they could potentially enter. We chose to use the deterministic model for this purpose so that all users saw the exact same past data before playing the game.

The game showed the user plots of harvest, estimated remaining biomass in the fishery, and profit vs. time. At the beginning of each turn of the game, the user entered an amount of biomass they wanted to harvest into a textbox, clicked enter, and then the remaining biomass, post-harvest, grew according to the models that governed the simulated fishery, and the result was displayed on the screen numerically. In addition, all plots updated, adding the players harvest choice to the harvest plot, the resulting biomass to the biomass plot and the new accumulated profit to the total profit plot. See figure 4.1 for a picture of the game display.

The the user's score was the discounted net profit accumulated over the game, with a discount rate of 0.03 and a constant price of 10,000 dollars per ton of biomass caught. In addition, the user received a bonus added to their score at the end of the game, which was the discounted profit that would have been generated by harvesting all of the remaining biomass left in the fishery after the game was over. The bonus prevents optimal users from harvesting everything on the last turn. Without adding the bonus, the user's score would be highly

sensitive to their last harvest decision. This bonus is explained to the user in the game directions (see section 7.2).

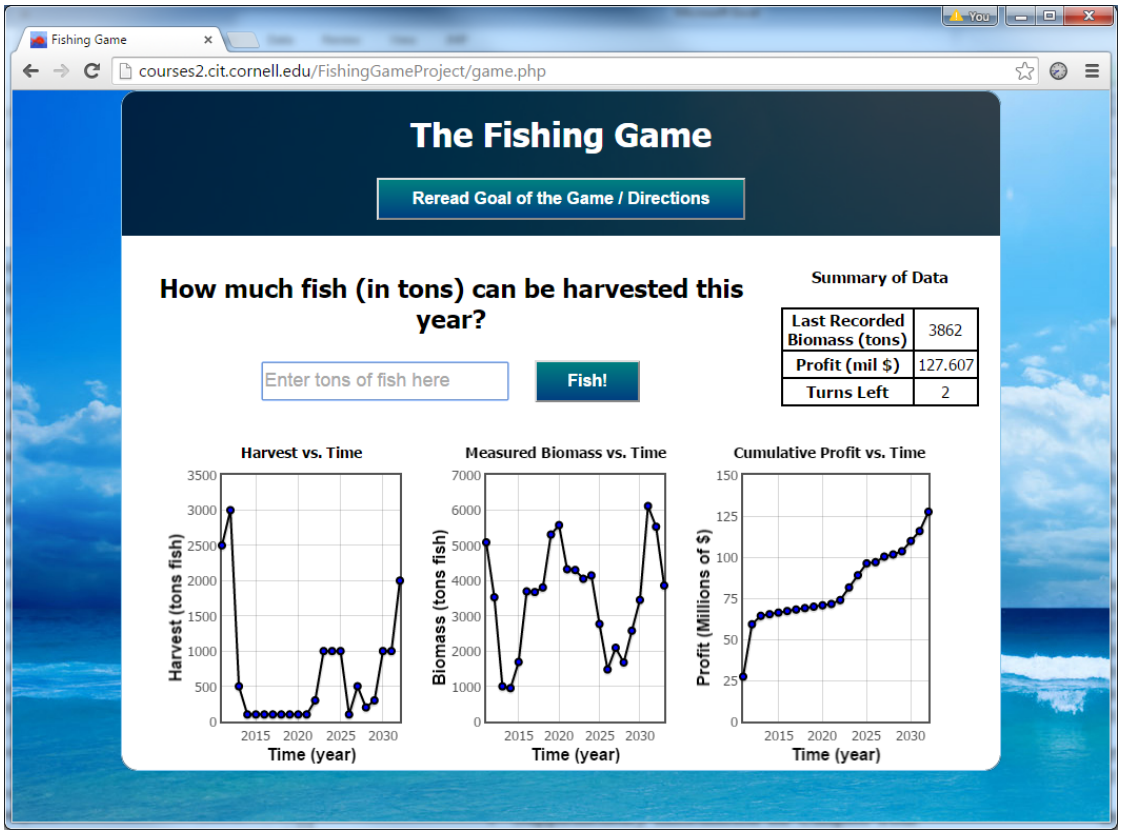

Figure 4.1: Game play for the unstructured herring fish game.

After a student completed their last turn, the game displayed their score in addition to a leaderboard, which included the scores and initials of the top players in the class, up to that point in time. The leaderboard provided an external incentive to play well. However, the students did not receive a course grade or monetary incentives based on performance.

Throughout the game, data was stored locally on the user's computer using

cookies. Upon exiting the game, this anonymous data was then sent to a server, using PHP (a server-side programing language for web development, Welling and Thomson, 2003), and stored in a database. This data included the time the user finished playing the game, an anonymous user ID number, the student's answers to the survey questions, the environmental noise variable σ, total profit (i.e. "points") and their time series of harvest decisions, resulting biomasses, realizations of environmental noise and measurement error, and in addition the analogous data from their practice game. By recording the environmental noise and measurement error time series data, experienced by the user, we were able to compare how any strategy (in our case strategies generated by optimization models) would have performed playing that user's exact instance of the game.

After playing the unstructured herring game, the student was directed via a link to the salmon game. Using cookies, the anonymous user ID number from the herring game was saved and recorded along with a unique user ID number for the salmon game as well. In the salmon game, the fishery population dynamics were age-structured, so the game directions also included information on the salmon's life cycle, which consisted of juvenile (1 year-old) and immature (2 year-old) fish survival and growth and adult fish (3 year-old) reproduction. On each turn of the game, the user entered the biomass of adult and immature fish they chose to harvest in two side-by-side textboxes. Plots of the student's harvest and biomass time series data were the same as for the herring fishery, except now each plot had two curves, one for immature fish and one for adult fish. The user could not observe or harvest juvenile biomass. See figure 4.2 for a picture of the game display in the age structured game.

The user's score in the age-structured game was similar to the unstructured

game, except discounted net profit was summed over both adult and immature harvest, and the bonus was the discounted profit that would have been generated by harvesting all of the remaining adult biomass for three years after the game was over (it takes 3 years for the recruits at the end of the game to return to be harvested as adults).

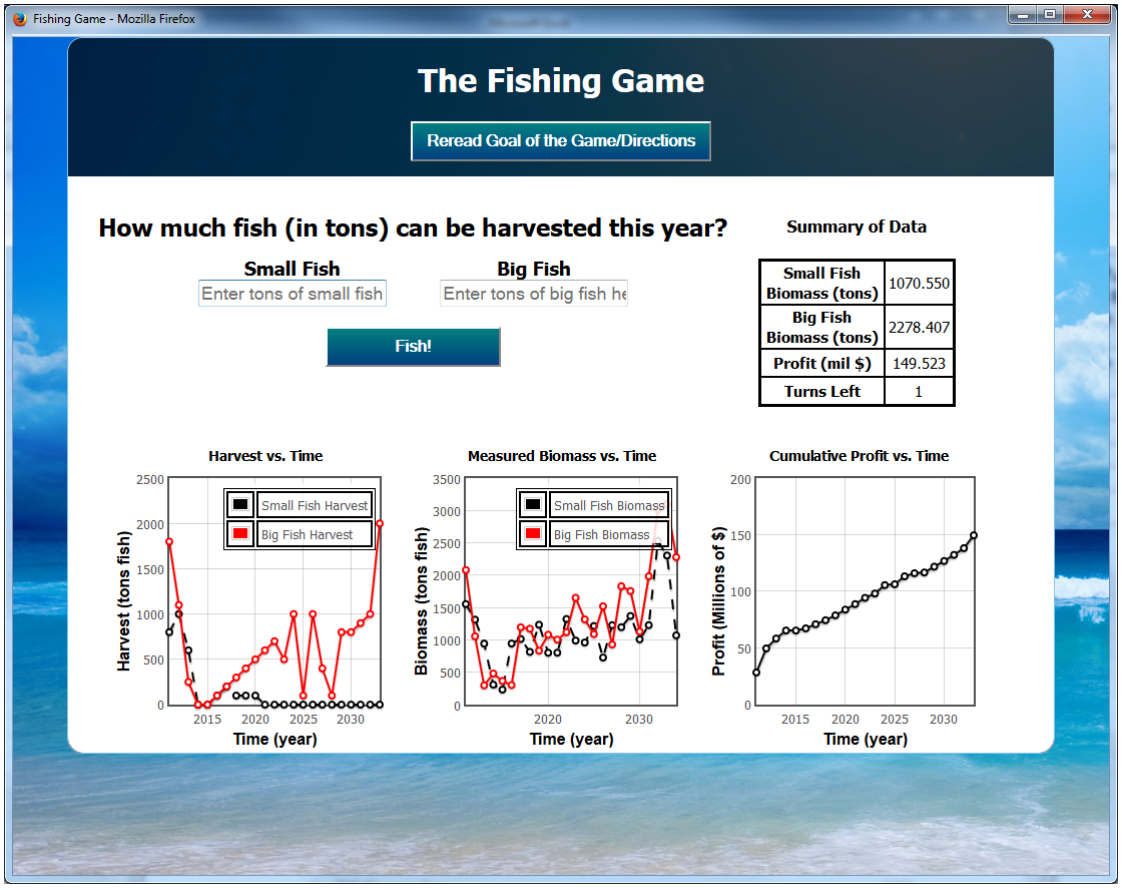

Figure 4.2: Game play for age structured salmon fish game.

Another goal of this study was to collaborate with instructors to incorporate the game into their curriculum to facilitate active learning. Therefore, while the

students played each version of this game multiple times, for pedagogical reasons, students were only asked to try their hardest to score the most amount of points possible during their first game. After everyone had finished their first game, they were allowed to collaborate and experiment, to facilitate students learning the principles of conservation biology, and therefore we did not include the students' latter turns in the analysis.

4.2.2 Simulated population dynamics

The herring fish game was governed by a simple unstructured, one dimensional model, where the manager chooses to harvest h_t tons of biomass in year t, and the resulting biomass in year $t+1$, B_{t+1}, is a nonlinear function of the biomass that escaped harvest in year t, $R(B_t - h_t)$, times a log-normally distributed random number, z_t, with mean one and standard deviation σ [1]

$$B_{t+1} = z_t R(B_t - h_t). \tag{4.1}$$

We choose R to be the Beverton-Holt recruitment function, to exclude the possibility of complicated chaotic and periodic dynamics in the absence of harvest,

$$R(B) = \frac{b_1 B}{1 + b_2 B}, \tag{4.2}$$

where b_1 is per unit biomass recruitment at low densities and b_2 controls the carrying capacity of the population.

[1] In standard log-normal notation this means $z \sim \ln\mathcal{N}(\ln(1/\sqrt{1+\sigma^2}), \sqrt{\ln(1+\sigma^2)})$. In other words, the mean of the lognormal random variable is one, the mean of the log transformed variable, μ, is actually negative.

The manager observes a stock biomass of $m_t B_t$, in year t, where m_t is a log-normally distributed random variable with mean one and standard deviation 0.025. In other words, the user experiences a measurement error of $m_t - 1$ in year t.

The age structured fish game is based on the life cycle of Coho Salmon, including three independent cohorts that undergo a three stage life cycle. Juvenile fish live in the river and survive and grow into small fish which swim downstream to the ocean where they mature, and finally they swim up stream to spawn and die. The manager sets a total allowable catch (which is perfectly realized) of $h_{2,t}$ for immature fish and $h_{3,t}$ for adult fish. Adult fish harvest occurs prior to recruitment.

$$\begin{aligned} B_{1,t+1} &= z_t R(B_{3,t} - h_{3,t}) \\ B_{2,t+1} &= z_t a_{21} B_{1,t} \\ B_{3,t+1} &= z_t a_{32}(B_{2,t} - h_{2,t}). \end{aligned} \tag{4.3}$$

We parameterized the two models by starting with rough estimates from the literature and then adjusted the values so that the growth rate of our hypothetical herring (unstructured) and coho salmon (age-structured) populations matched. The average 3 year old coho salmon weighs 8.0 pounds and the average 2 year old salmon weighs about 3.1 pounds (Marr et al., 1944). A typical survival probability for pacific salmon populations is 0.8 in good years and 0.28 in bad years (Worden et al., 2010). Hence, we fixed $a_{32} = (8lbs/3.1lbs)(0.8 + 0.28)/2 \approx 1.4$. Coho salmon are more productive than Herring at low densities, hence we chose to lower salmon recruitment as much as "believably" possible so that the growth rate in our salmon and herring fisheries matched. To do this, we assumed the average survival probability of juvenile salmon was equal to the estimate for

bad years (0.28). Therefore, with the composite parameter of recruitment at low densities estimated in (Worden et al., 2010) of 60 juveniles per spawner, we get $a_{21}b_1 = (0.28)(60 recruits/spawner)(spawner/8lbs)(3lbs/recruit) \approx 6.6$. We chose a herring growth rate of 2.1 because $2.1^3 \approx (6.6)(1.4)$. The growth rate reported for herring population dynamics ranges from $1.4 - 1.8$ (Bjørndal and Conrad, 1987; Nostbakken and Bjorndal, 2003), so while our herring growth rate is high, it is not unreasonably so. Carrying capacity is arbitrarily set to $5,400$ tons, which determines b_2 for both models.

4.2.3 Optimal strategies and statistical analysis

We calculated optimal strategies using (Reed, 1979) for the unstructured model and the results from Chapter 3 for the age structured model. For the parameters in the game, the optimal escapement is 2049 tons of fish, in the unstructured game, and 556 tons of adult fish in the age structured game.

The first goal of the experiments was to compare the performance of users to fitted models playing the exact same instance of the game. As a control, we compared both the fitted models' and users' performance to the net discounted profit generated by the optimal constant escapement rule specified above (i.e. the optimal strategy with perfect information).

For all fitted models, parameters were initially estimated using the data generated from the users' eight turn practice game. In the computer's first turn of the game, it harvests using the best escapement rule assuming these parameter estimates are true. After observing the stock biomass resulting from its previous harvest, it re-estimates the parameters using the previous data along with this new

data point. It then chooses a new escapement rule based on the new parameter estimates, and the process is continued until the game is over.

The parameter estimation for the unstructured game is performed by minimizing sum of squared errors between the log transformed recruitment data, $\log[m_{t+1}B_{t+1}]$, and log transformed predicted recruitment under the model, $\log[R(m_tB_t - h_t)]$, using the function `lsqcurvefit`, an implementation of the trust-region-reflective algorithm, in `MATLAB` (MATLAB, 2010). For the age structured game, since juvenile biomass is unobservable, the procedure is the same as above, except predicted recruitment is $a_{21}R(m_{3,t}B_{3,t} - h_{3,t})$ and observed recruitment is $m_{2,t+2}B_{2,t+2}$. The transition between immature and adult biomass is estimated similarly.

We consider fitted models with the same functional form (Beverton-Holt recruitment) as the model underlying the simulated population dynamics, and in addition models that incorrectly specify the functional form (discrete logistic and Ricker recruitment). For the age structure game we also consider developing escapement rules from an unstructured Beverton-Holt recruitment model (as in (4.1)). To estimate the parameters for this model, the computer minimizes the sum squared error between the log transformed aggregate biomass data, $\log[m_{2,t+1}B_{2,t+1} + m_{3,t+1}B_{3,t+1}]$, and the predicted biomass, $\log[R(m_{2,t}B_{2,t} + m_{3,t}B_{3,t} - h_{2,t} - h_{3,t})]$. It then harvests the two age classes in proportion to their respective observed biomasses.

The second goal of the experiments was to analyze what strategies the users were deploying and how well different strategies performed compared to others. We compared the user's behavior to three idealized candidate strategies, constant harvest, proportional harvest and constant escapement. Constant harvest means

the user enters the same harvest at every time step (harvest = β, where β is the user's mean harvest). Under a proportional harvest strategy the user harvests a constant proportion of the biomass (harvest = $\beta\cdot$ biomass, where β is their harvest proportion). Constant escapement, means the user lets a constant amount of biomass escape harvest (harvest = 0 if biomass $\leq \beta$, harvest = biomass $-\beta$ if biomass $> \beta$, where β is the biomass they let escape harvest). After fitting these three models to the harvest vs. biomass data generated by each user during their game play, the users were categorized into the three strategy classes based on which model fit had the lowest sum squared error. For the age-structured game we repeated the above analysis on adult harvest, for simplicity (since adult harvest is optimal), but the results reported in the next section are similar if total harvest of both age classes is used instead.

4.3 Results

4.3.1 Unstructured population game

All human subjects achieved less discounted net profit than would be achieved using the optimal constant escapement strategy with known parameters (Fig. 4.3a). The average human scored 65.4 percent of the discounted net profit generated using the optimal constant escapement strategy, and 11.0 percent of humans achieved over 90 percent of this optimal expected net profit.

Most users performed worse than the escapement rules generated from the fitted models (Fig. 4.3bcd) even if the model made incorrect assumptions about the underlying recruitment function (Fig. 4.3cd).

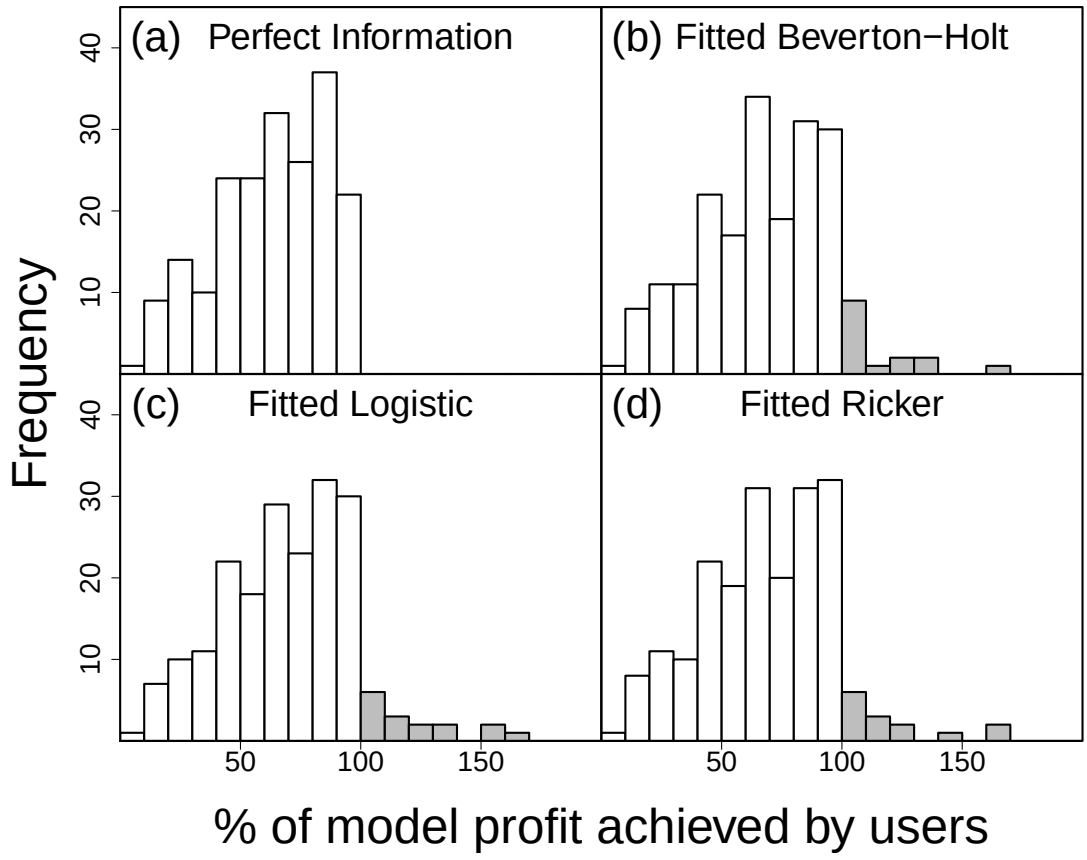

Figure 4.3: The percent of the mathematical model's total profit achieved by the user, in the unstructured game, when the mathematical model is (a) Beverton-Holt with true parameters, i.e. perfect information (b) Beverton-Holt but with parameters estimated from the data, (c) discrete logistic with parameters estimated from the data and (d) Ricker with parameters estimated from the data. For example a value of 50 percent means the user generated half the profit the mathematical model did managing the exact same instance of the game. A value of 200 percent means the user generated twice as much profit as the model.

When fitting a linear model, using `lm` in `R` (R Development Core Team, 2008), to test whether the percent of optimal profit achieved by the user was cor-

related with the answers to the survey questions, standard deviation of environmental stochasticity, and net profit generated during the practice game, not including the bonus, practice game profit was the only significant predictor [2] ($p < 0.0001$). Doing a simple linear regression for the user's percent optimal profit vs. practice game score, the model explained 28 percent of the variation in the users optimal profit, ($R^2 = 0.28$, see Fig. 7.4 on pg. 124).

When the practice game predictor was removed from the linear model, the user's level of study (freshman, senior, PhD etc.), academic field of study, and standard deviation of the observed environmental stochasticity, still did not significantly correlate with the user's performance. Two predictors were significant in this model. The five students that indicated "I am considering a career in fisheries management, but have no experience" generated more profit than students that responded "I am not considering a career in fisheries management" (p = 0.033) and students in Cornell's "Environmental Conservation" course scored significantly higher than the students in Ithaca College's "Principles of Biology" course (p = 0.041). However, a linear model with just these two predictor variables only explained four percent of the variation in user performance. It should also be noted that if we grouped the two students that actually had fisheries management experience with those five students that indicated a career interest but no experience, the answer to the management experience question would no longer significantly correlate with the users' scores. This suggests the sample size for students who were considering careers in fisheries management may be too small to draw any meaningful conclusions.

Classifying the humans' harvest strategies into the three categories: con-

[2]Because the practice game is only 8 turns, the bonus is a very large proportion of the subject's practice game score. Therefore, including the bonus washes out the effect of the users' strategies over the course of the practice game.

stant harvest, proportional harvest and constant escapement, people harvested a constant proportion of the observed biomass (129 users) much more often than allowing a constant amount of biomass escape harvest (30 users) (Fig. 4.4). Many users repeated their harvest decision from the previous turn and the average user only entered 10 unique harvest values over the course of the 21 turn game (Fig. 7.5 on pg. 125), but only 39 users were classified as constant harvesters. All five users that indicated a career interest in fisheries management were classified as proportional harvesters. Of the two users with actual management experience, one was a constant harvester and the other was a proportional harvester.

Nearly an equal number of humans over-fished the population vs. under-fished the population (Fig. 4.5a). If we define under-fishing as letting on average more than $(1+q)S^*$ fish escape harvest and overfishing as letting less than $(1-q)S^*$, fish escape harvest, where S^* is optimal constant escapement under perfect information, nearly an identical proportion of the humans are under-fishers as over-fishers for all $q < 0.6$. For example, if $q = .5$, there were 66 over-fishers, 63 under-fishers, and 70 humans whose median escapement was within 50 percent of the optimal value (Fig. 4.5a).

Students who used constant escapement strategies were more likely to over-fish (circles in Fig. 4.5a). Proportional harvesters both over and under-fished (triangles in Fig. 4.5a) and constant harvesters were much more likely to under-fish (pluses in Fig. 4.5a). Note that constant harvesters really can only under-fish because if they were to over-fish the biomass would eventually decrease to the point where their constant harvest would deplete the fishery, at which point they would have to abandon the constant harvest strategy.

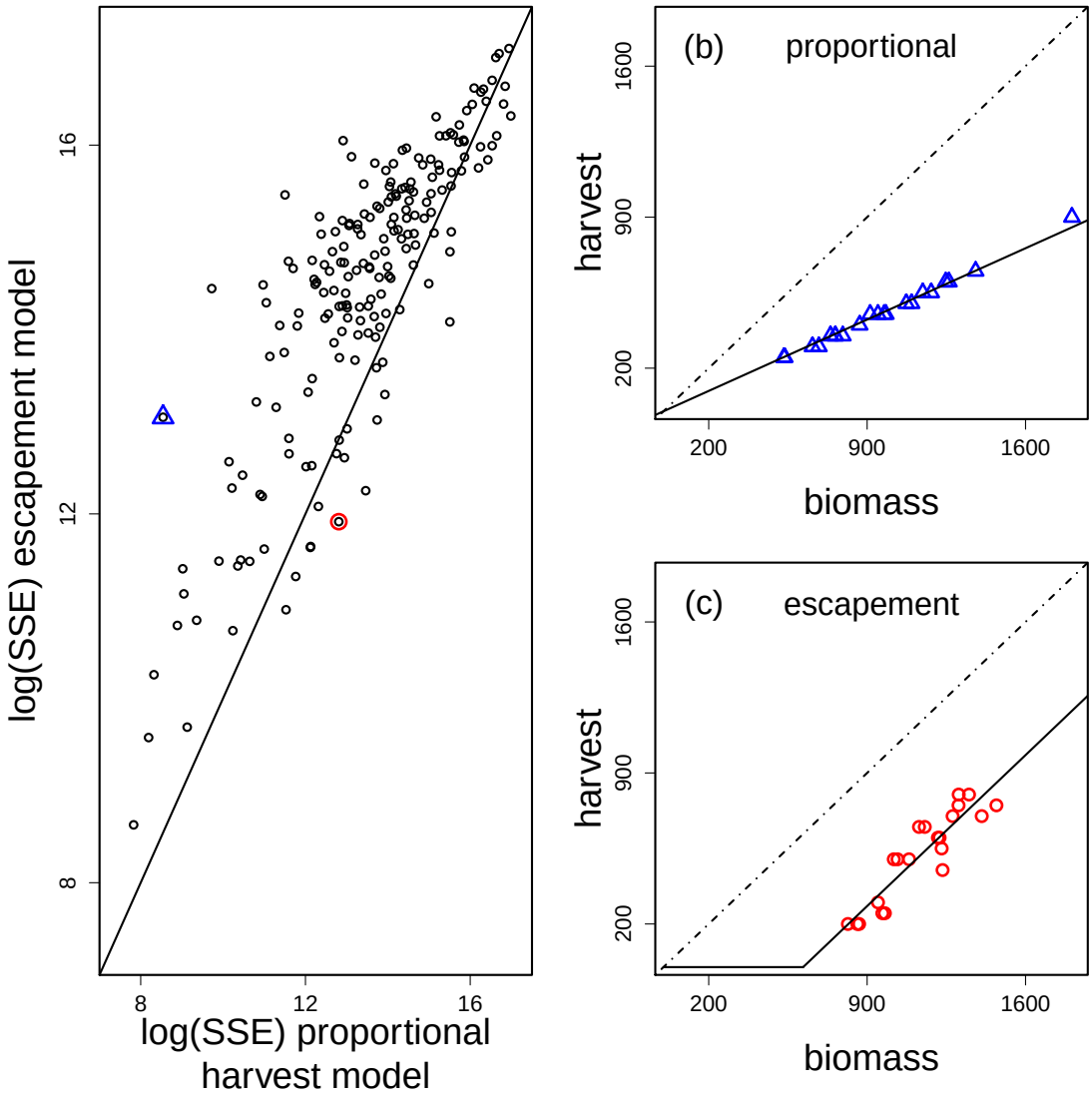

Figure 4.4: (a) the sum of squared error when fitting each user's harvest data, in the unstructured game, to a constant escapement model vs. fitting a proportional harvest model on a log-log scale. Points to the right of the 1:1 line represent users whose variation in harvest is better explained by constant escapement than proportional harvest. (b-c) The harvest vs. observed biomass for a user (highlighted with a blue triangle in a) deploying a proportional harvest strategy (b) and a constant escapement strategy (c).

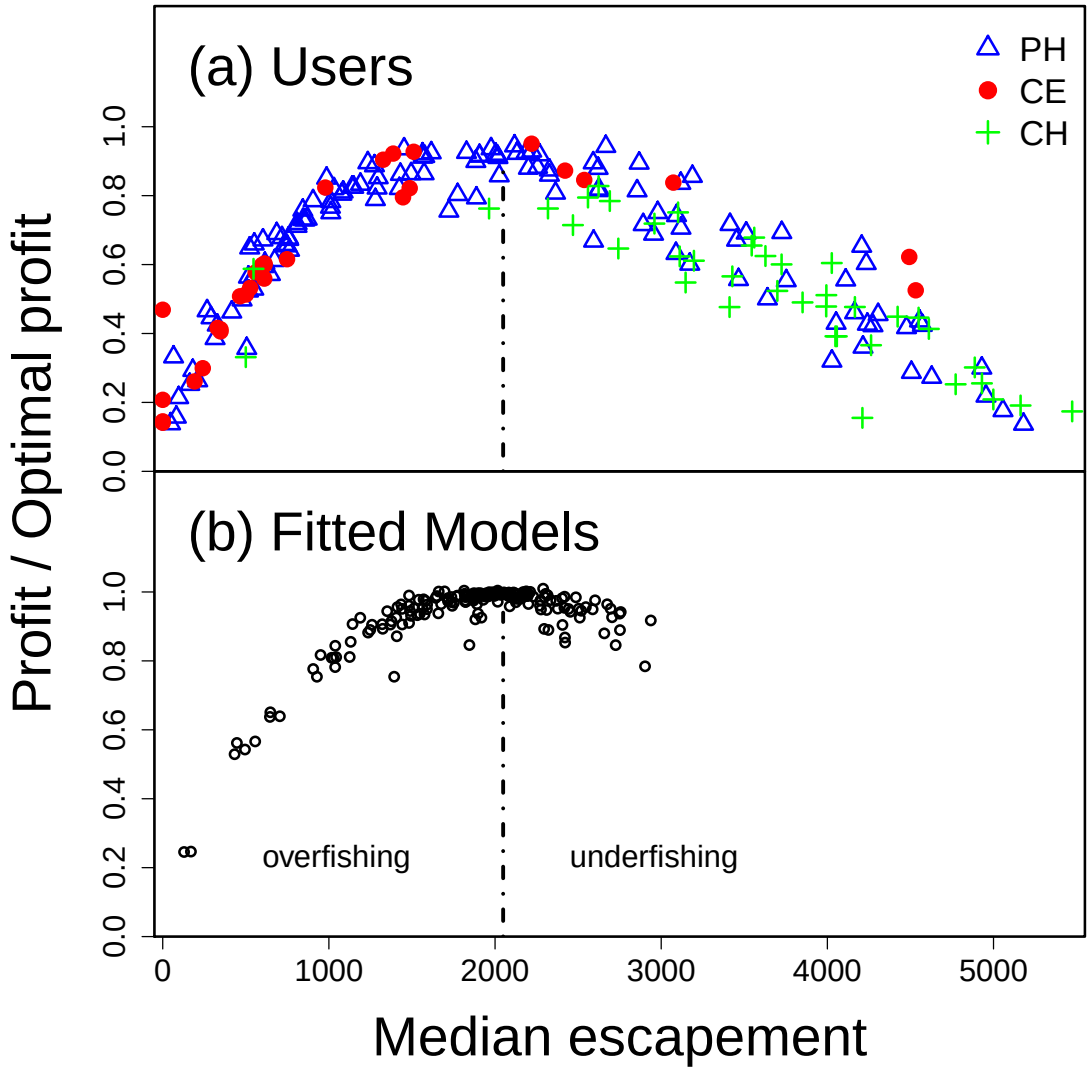

Figure 4.5: (a) The profit generated by each user, in the unstructured game, relative to the net profit the optimal strategy with perfect information would generate in the corresponding instance of the game, as a function of the average amount of fish the user let escape harvest. The red circles, blue triangles and green pluses are for users who used constant escapement (CE), proportional harvest (PH), and constant harvest (CH) strategies, respectively. (b) the analogous proportion of optimal profit generated by the fitted model vs. the median of escapements chosen by the model after it fit a recruitment function to the data during each turn of the game. The dotted line is optimal escapement strategy under perfect information.

Poorly performing harvest rules generated by the fitted Beverton-Holt recruitment model were much more often due to overfishing than under-fishing (Fig. 4.5b). Poor model performance was due to two reasons: (1) during the practice game the user allowed similar amounts of biomass to escape harvest on every turn, generating poor data for model fitting, and (2) the standard deviation of the environmental noise was high (Fig. 4.6). When these conditions are true the data can misrepresent the recruitment function (Fig. 4.6b compared to 4.6c) and lead to a poor escapement strategy. Despite the poor escapement strategies that sometimes resulted from the fitted models, they still were less frequent and generated more long term discounted profit than the worse users (compare the low points in Fig. 4.5a to 4.5b).

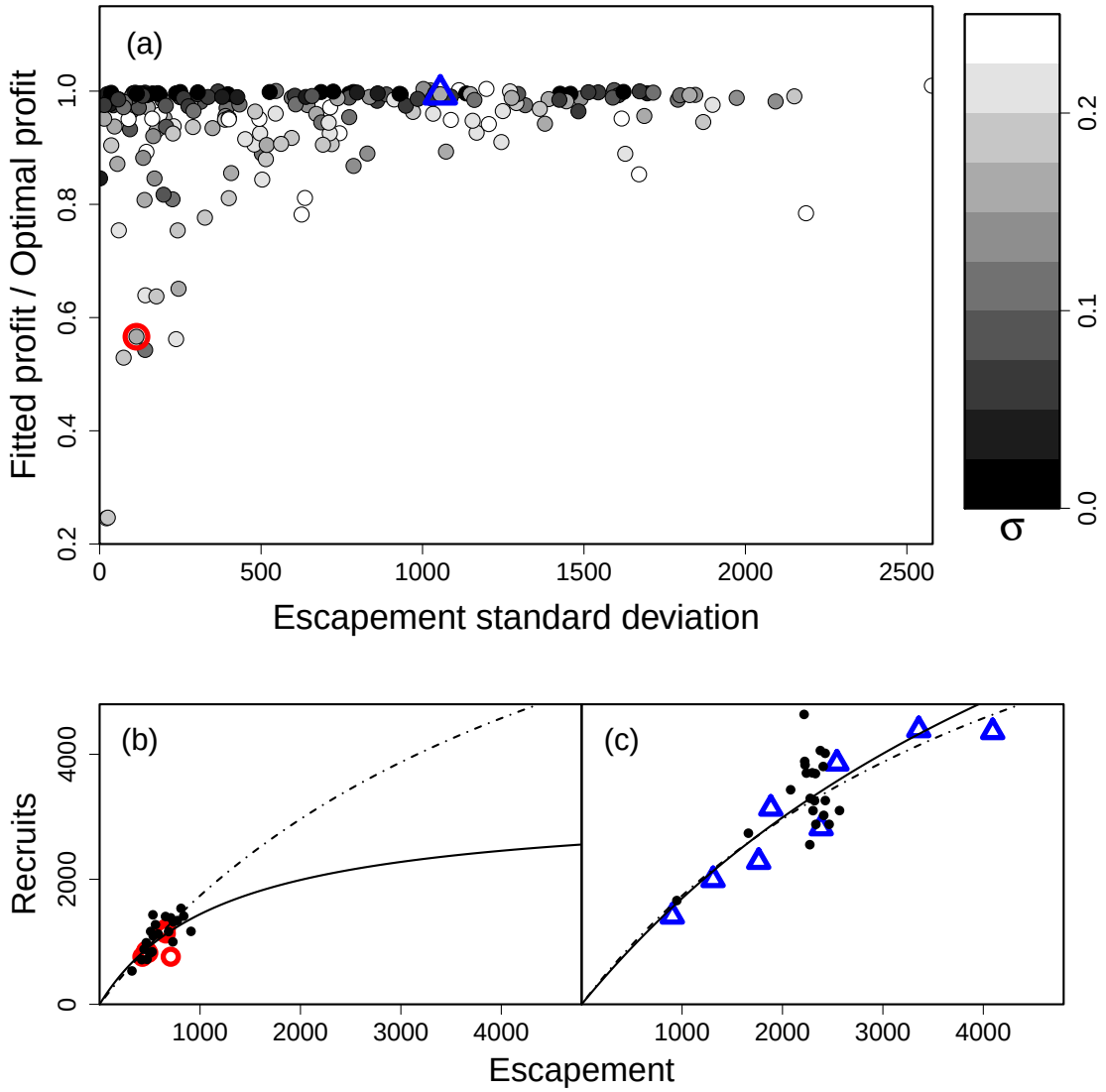

Figure 4.6: (a) The profit generated from the strategies using the fitted Beverton-Holt model relative to the optimal profit under perfect information, as a function of the standard deviation in practice game escapement, generated by the user. Dark and light circles are for instances of the games with low and high levels of environmental stochasticity respectively. (b-c) The true recruitment function (dashed line) and fitted recruitment function (solid line) for two instances of the game, [these examples are highlighted by a red circle and blue triangle in (a)], where the fitted model generates unprofitable escapement strategies (b - red circle) and profitable ones (c - blue triangle). The open symbols are recruitment data generated by the user in the practice game, while the smaller filled points are generated by the fitted model when playing the actual game.

4.3.2 Age structured population game

In the age structured model, the average user achieved 63.6 percent of the optimal profit achieved by a model with perfect information. The most profitable user scored only 84.3 percent of the optimal profit, in comparison to the best performer in the one dimensional game who scored over 95 percent of optimal profit. On the opposite end of the spectrum the worst users in the one dimensional game only scored 7.2 percent of optimal profit while in the age structured game the worst user scored 11.8 percent of optimal profit. A full distribution of the relative performance of the users compared to the optimal policy in the age structured game is given in Fig. 4.7. The reason for the improved performance by the worse players, despite the age-structured game being more complex, was due to the fact that this game includes three independent cohorts. Even if one or two cohorts were driven to low levels, some harvest could be achieved in the remaining turns as long as one cohort remained. A player could make one very bad decision, and learn from it, without collapsing the entire fishery.

The user's performance in the age structured game was mainly determined by their overall fishing pressure and not their decision of which age class to fish (compare Fig. 4.8a to 4.8b). The majority of users harvested more immature biomass than adult biomass, despite exclusive adult harvest being the optimal strategy (4.8b). Similar to the simple unstructured, one dimensional game, users who deployed a constant escapement strategy (for adults) were more likely to over-fish (4.8a).

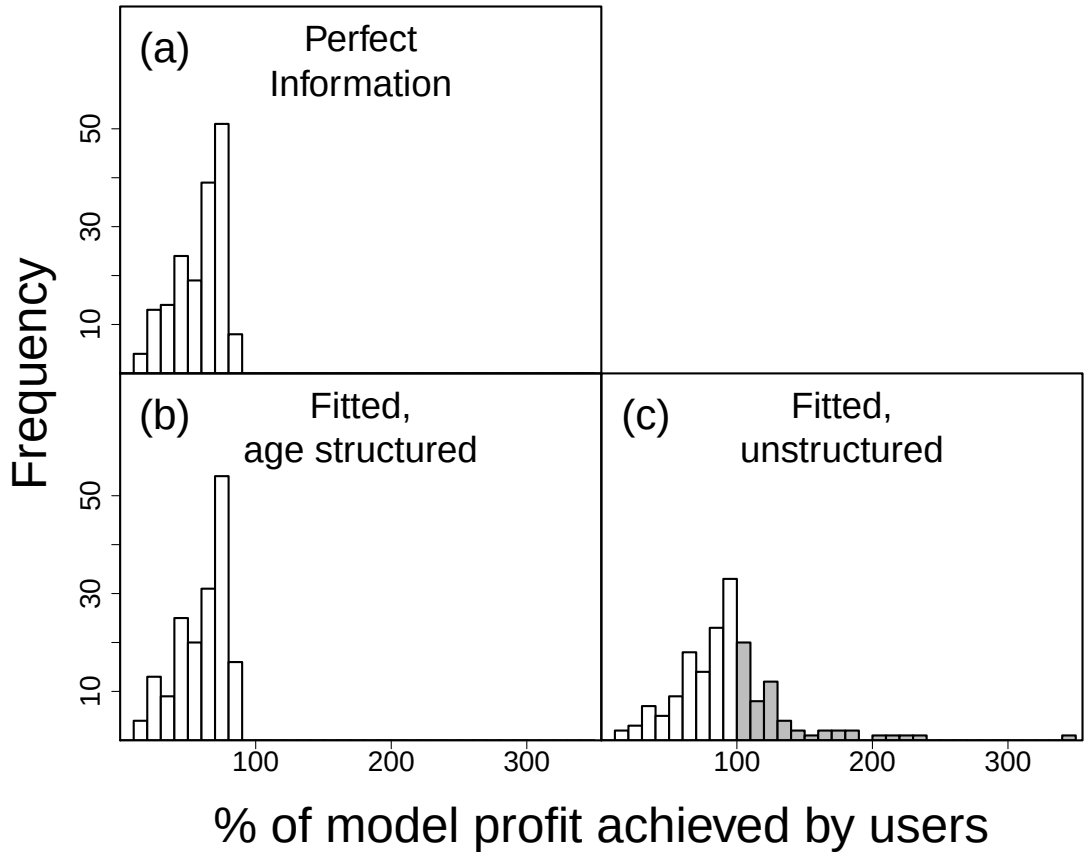

Figure 4.7: The percent of the mathematical model's total profit achieved by the user, in the age structured game, when the mathematical model is (a) age structured with true parameters, i.e. perfect information (b) age structured but with parameters estimated from the data, and (c) unstructured with parameters estimated from the aggregated (immature + adult) biomass data. For example a value of 50 percent means the user generated half the profit the mathematical model did, managing the exact same instance of the game. A value of 200 percent means the user generated twice as much profit as the model.

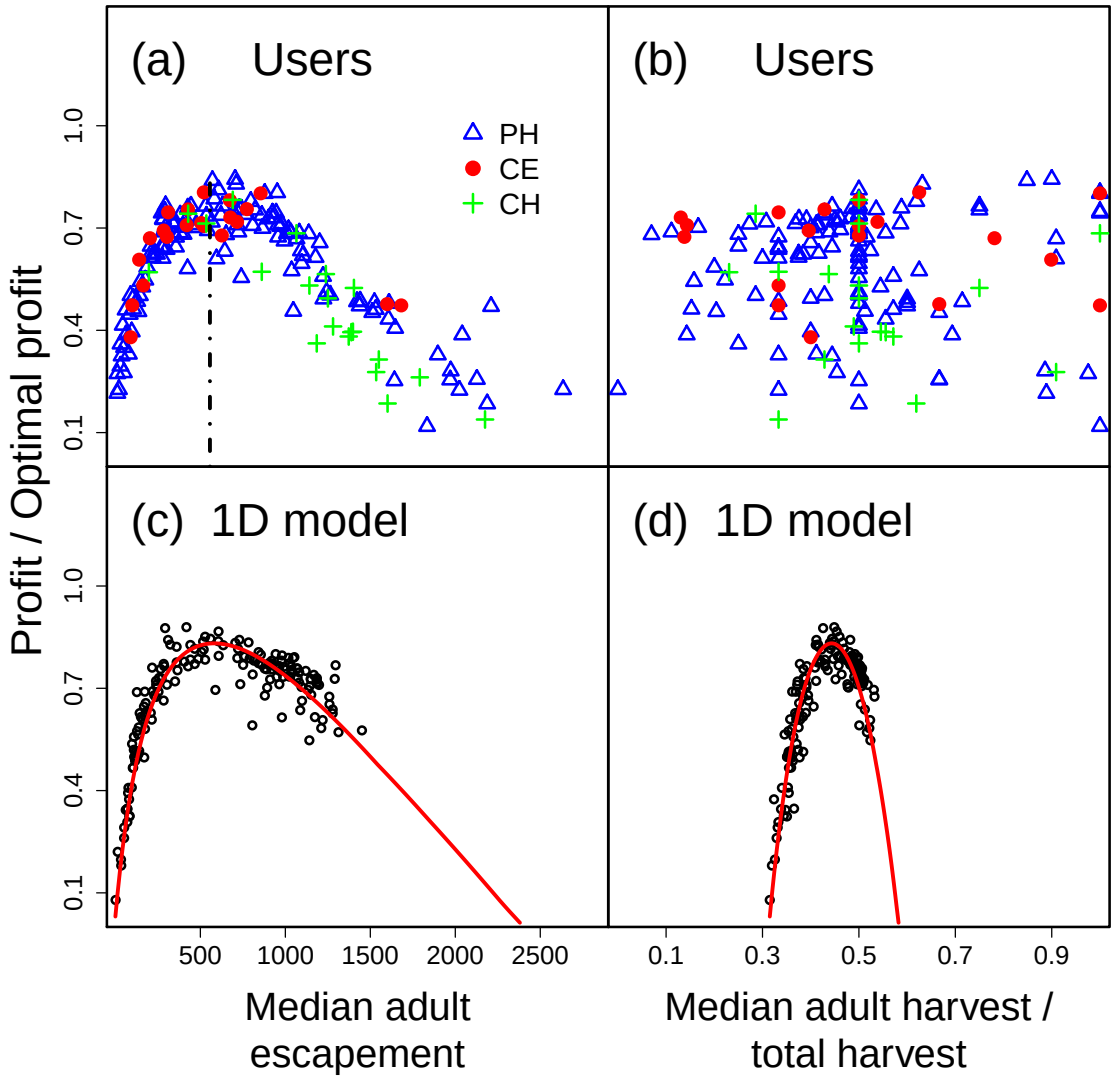

Figure 4.8: (ac) The proportion of optimal profit, in the age structured game, generated by the (a) user and (c) fitted unstructured model for each game as a function of the average escapement chosen. (bd) The proportion of optimal profit generated by the (b) user and (d) fitted unstructured model as a function of the average proportion of harvest allocated to adult biomass during the game. The red lines represent the percent of optimal profit we would expect to generate using a constant escapement strategy ($\tilde{s}$ in equation (4.4)), assuming deterministic population dynamics.

The average escapement strategies resulting from the fitted age structure model achieved 98.4 percent of the optimal profit, even better than in the unstructured game. Even in the fitted model's lowest performing game, it achieved 78.9 percent of optimal discounted net profit, far better than even the median user. This is for two reasons (1) users in the practice game tended not to let the same amount of adult fish escape harvest every turn, producing good data for model fitting, and (2) the transition rate from immatures to adults was always estimated well, because it is a single parameter that can be estimated independently from recruitment, while the recruitment function requires two parameters to be estimated simultaneously. The result of point (2) is that the models always fished from the correct age class.

The average escapement strategy, generated by fitting a one dimensional unstructured population model to the aggregate age-structured data, achieved 72.3 percent of the optimal profit. This represents a 13.5 percent gain in profit over the average human operating solely on intuition. Only 58 users, out of 172, generated more profit than would have been obtained by harvesting based on the fitted unstructured model. However, for instances of the game where the unstructured model generated low discounted net profit, the model's proposed escapement rule nearly wiped out the fishery, by letting very little biomass escape harvest. These strategies generated less discounted net profit than the least profitable users (compare the lowest points in Fig. 4.8a to 4.8c).

In Fig. 4.8d there is a correlation between the proportion of harvest from the adult class and total profit, despite the fact that the fitted one dimensional escapement strategy harvests from the adult and immature classes proportionally according to their biomass. To see why, consider a deterministic version of the

age structured population dynamics, and assume the manager always allows $\tilde{s}$ total biomass to escape harvest, targeting each age class proportional to it's corresponding biomass. In addition, assume $\tilde{s}$ is smaller than the equilibrium biomass under no harvest, so that the dynamics do not allow for letting more biomass escape than is present at equilibrium. Then the dynamics are,

$$\begin{aligned} B_{1,t+1} &= R(\tilde{s}r_t) \\ B_{2,t+1} &= a_{21}B_{1,t} \\ B_{3,t+1} &= a_{32}\tilde{s}(1-r_t). \end{aligned} \tag{4.4}$$

where $r_t \equiv B_{3,t}/(B_{3,t}+B_{2,t})$, is the biomass ratio in year t. Note that with harvest proportional to the respective age classes, the biomass ratio is equivalent to the ratio of adults harvested and also the ratio of adult biomass that escapes harvest. At equilibrium, $r_{t+1} = r_t \equiv r$, is the solution to

$$r = \frac{a_{32}\tilde{s}(1-r)}{a_{21}R(\tilde{s}) + a_{32}\tilde{s}(1-r)}. \tag{4.5}$$

For Beverton-Holt recruitment, r is the root in $[0,1]$ of the cubic polynomial,

$$[b_2\tilde{s}]\,r^3 + \left[1 - 2b_2\tilde{s} - \frac{a_{21}}{a_{32}}b_1\right] r^2 + [b_2\tilde{s} - 2]r + 1. \tag{4.6}$$

When fishing pressure is low (i.e. in the limit as $\tilde{s} \to 0$) the cubic term becomes negligible and therefore,

$$r = \frac{a_{32}(1 - \sqrt{a_{32}a_{21}b_1})}{a_{32} - a_{21}b_1}. \tag{4.7}$$

When there is no fishing pressure,

$$r = a_{32}/(a_{32} + 1) \tag{4.8}$$

Substituting the parameters from the game into the above formulas, 32 percent of harvested biomass is from the adult class when fishing pressure is high (from equation (4.7), low escapement), and 58 percent of total harvest is from adult biomass under almost no fishing pressure (from equation (4.8), high escapement). This makes sense, since under high fishing pressure low adult biomass leads to greater per capita recruitment and hence the fishery is dominated by immatures. These calculations match the range of adult harvest proportions observed in Fig. 4.8d, since the minimum harvest value in the plot is the minimum harvest proportion we calculated under high fishing pressure, 32 percent. Note that in this game it is always optimal to harvest adults, due to a high value of a_{32} and a low discount rate. Therefore, the fact that profit is not monotonically increasing with the allocation of harvest to the more valuable adult class, Fig. 4.8d, means the choice of escapement is the main driver of profit, not the resulting proportion of harvested biomass allocated towards adults, r.

Generating the full range of possible escapement values, zero to the total biomass under no harvest, and calculating corresponding proportion of optimal harvest using (4.4), gives the red curve in Fig. 4.8c. In addition we can calculate the corresponding r for each escapement value, numerically, using (4.6), which gives the red curve in figure 4.8d. This shows that r only explains the profits generated by the fitted unstructured model through its correlation with total escapement, not because the harvest proportion, resulting from the unstructured model, explicitly predicts profit.

4.4 Discussion

Many mathematical tools exist to improve decision making in environmental management, including methods from optimization and optimal control. Yet managers are still resistant to using these tools to develop management plans. At least one reason for this is that it is often unclear what a manager may gain by using quantitative methods, especially if the dynamics of the managed system are not well understood.

In this chapter we looked at optimal escapement strategies for the management of simulated fisheries, developed using highly simplified models of fish stock dynamics, and tested their performance compared to humans managing the simulated population using only their experience and judgment. The models, performed better than the users, *on average*, even when the models mis-specified recruitment or state variables. However, in the age structured game, the worst outcomes produced by the simplified unstructured model were worse than the worst outcomes generated by the users.

Users and fitted models tended to make different types of mistakes. An equal number of users overfished vs. underfished the stock. However, when the models failed it was almost always due to overfishing.

We found that even when the model is perfectly specified, and only needs to fit parameters from the data, it still can perform worse than a human using intuition alone, especially when environmental stochasticity is high and prior management decisions have all been similar. This suggests that passive adaptive management, choosing the best strategy, based on the current knowledge of the system, to optimize some objective, without any regards to the information gained

by deploying that action (Williams, 2001), can lead to poor performance. This problem is likely common in fisheries management, since overexploited fisheries are ubiquitous, and therefore the time series data of fish stock abundances may often contain only population sizes well below carrying capacity. In such cases, recruitment curves may often be incorrectly estimated and our simple models will naively suggest that it is optimal to keep overfishing.

Our results suggest that probing the system by performing an action that is suboptimal given the manager's current belief about the system, but that will reveal information that improves management in the future might be ideal in such scenarios. Incorporating the economic benefits of learning from experimentation explicitly into the optimal decision problem, known as *active* adaptive management, has been studied within the context of harvested populations. However, due to computational limitations solutions are always limited to cases with one of the three following assumptions: (1) both the probability distribution specifying environmental stochasticity and all parameters in the recruitment function are perfectly known, except for a single parameter to be estimated from the data (Walters, 1981; Ludwig and Walters, 1982), (2) there is a small number of candidate models, with all parameters fixed within each model (Williams, 2001), or (3) only a small number of actions and system states are admissible (i.e. action = harvest or not, fishery state = robust, vulnerable, or collapsed, Hauser and Possingham, 2008).

Unfortunately, the problem of choosing an optimal escapement level in our game, using the principles of active adaptive management, is computationally infeasible given current algorithms and computing power because our game allows for an infinite set of possible actions and states, governed by unknown parameters

and unknown variability in environmental noise.

It is rather alarming that even in the most optimistic case, where the underlying dynamic model is known and parameters have to be estimated from the data, passive adaptive management can fail to achieve desirable results. However, the alternative of letting humans manage our simulated fishery based solely on their experience and judgment typically led to much worse outcomes. Because mathematical models usually improved management outcomes in our experiment, we would recommend modeling be more widely adopted in management. However, models should not be considered as a replacement for manager expertise. Our results show that in some cases human intervention will be required when models appear to recommend risky management decisions.

CHAPTER 5

SUPPLEMENTARY INFORMATION FOR CHAPTER TWO

5.1 Appendix A: Mathematical analysis

Since $A(t) + U(t) + D(t) + O(t) = 1$, it suffices to study the 3-dimensional system

$$\frac{dx(t)}{dt} = g(x(t), s(t)) \tag{5.1}$$

where $x(t) = (U(t), D(t), O(t))$ and

$$g(x, s) = \begin{pmatrix} \alpha - (\alpha + e_s s + 1)U + (\gamma - \alpha)O - \gamma OU - \gamma O^2 \\ e_s s(t)U - e_d D - D \\ U - e_o O \end{pmatrix} \tag{5.2}$$

with $A(t) = 1 - U(t) - D(t) - O(t)$. The goal is to find the sampling strategy, $s(t)$ that minimizes the objective function:

$$J = \int_0^T e^{-\delta t} \left[k_u U + k_o O + k_d D + f(s)(A + U) \right] dt. \tag{5.3}$$

Define the set of all admissible sampling strategies as

$$S = \{s(t) \mid s \colon [0, T] \to [0, s_{max}] \text{ is Lebesgue measurable}\}.$$

Because the set of all Lebesgue measurable functions is a vector space, and $[0, s_{max}]$ is convex, S is convex.

Lemma 5.1. *$g(x, s)$ is Lipschitz continuous in $s \in [0, s_{max}]$ and Lipschitz continuous in $x \in [0, 1] \times [0, 1] \times [0, 1]$.*

Proof. The first part follows from g being linear in s and the second part follows from g being continuously differentiable for all x in the compact set $[0, 1] \times [0, 1] \times [0, 1]$. □

Theorem 5.1. *Given the objective functional* (5.3)*, subject to the constraint* (5.2)*, there exists an $s^*(t) \in S$, such that $J(s^*(t)) = \min\{J(s(t)) \mid s(t) \in S\}$.*

Proof. By definition, the integrand of (5.3) is convex on the convex, closed control set S. The state equations in (5.1) are linear in the control variables. By lemma 5.1, equation (5.1) is bounded by a linear system in the state variables. Therefore by theorem 4.1 in (Fleming and Rishel, 1975) we have the desired result. □

Theorem 5.2. *Given the optimal sampling effort, $s^*(t)$, and the corresponding solution to the dynamic equations* (5.2)*, there exists adjoint variables λ_u, λ_d and λ_o satisfying*

$$\begin{aligned}
\frac{d\lambda_u}{dt} &= -\frac{\partial H}{\partial U} + \delta\lambda_u = -k_u + (\alpha + e_s s + 1 + \gamma O + \delta)\lambda_u - e_s s\lambda_d - \lambda_o \\
\frac{d\lambda_d}{dt} &= -\frac{\partial H}{\partial D} + \delta\lambda_d = -k_d + f(s) + (\alpha + \gamma O)\lambda_u + (e_d + 1 + \delta)\lambda_d - \lambda_o \\
\frac{d\lambda_o}{dt} &= -\frac{\partial H}{\partial O} + \delta\lambda_o = -k_o + f(s) + (\alpha + \gamma U + \gamma D + 2\gamma O - \gamma)\lambda_u + (e_o + \delta)\lambda_o \\
\lambda_i(T) &= 0, \ \textit{for } i \in \{u, d, o\}.
\end{aligned} \tag{5.4}$$

Where H is the current value Hamiltonian:

$$
\begin{aligned}
H(U, O, s, \lambda_u, \lambda_o) = k_u U + k_o O + k_d D + f(s)(1 - D - O) \\
+ \lambda_u(\alpha - (\alpha + e_s s + 1)U + (\gamma - \alpha)O - \gamma OU - \gamma O^2) \\
+ \lambda_d(e_s s U - (e_d + 1)D) \\
+ \lambda_o(D + U - e_o O).
\end{aligned} \tag{5.5}
$$

In addition,

$$
s^*(t) = \begin{cases} 0 & : \bar{s}(t) \leq 0 \\ \bar{s}(t) & : 0 < \bar{s}(t) < s_{max} \\ s_{max} & : \bar{s}(t) \geq s_{max} \end{cases} . \tag{5.6}
$$

where

$$
\bar{s}(t) = \frac{e_s U(t)[\lambda_u(t) - \lambda_d(t)]}{2\epsilon[1 - D(t) - O(t)]} - \frac{k_s}{2\epsilon}.
$$

Proof. A version of Pontryagin's minimum principle for bounded controls (Lenhart and Workman, 2007) gives the existence of adjoint variables satisfying (5.4) and the following characterization of the control

$$
\begin{cases} s^*(t) = 0 & : \frac{\partial H}{\partial s} \geq 0 \\ 0 < s^*(t) < s_{max} & : \frac{\partial H}{\partial s} = 0 \\ s^*(t) = s_{max} & : \frac{\partial H}{\partial s} \leq 0 \end{cases} . \tag{5.7}
$$

Since

$$
\frac{\partial H}{\partial s} = (k_s + 2\epsilon s)(1 - D - O) + e_s U \lambda_d - e_s U \lambda_u,
$$

(5.6) follows. □

A mathematically equivalent formulation of (5.2) exists, using a discounted Hamiltonian and discounted shadow prices, where the first line of (5.5) would be multiplied by $e^{-\delta t}$ and the adjoint equations would not include $\delta\lambda$ terms. In such a case $\lambda_u(t)$ is the amount of money a manager would be willing to pay at time zero to reduce Undetected patches at time t by a small amount. We chose the formulation where the adjoint variables are interpreted as the amount the manager would pay at time t rather than at time zero.

Lemma 5.2. *The integrand in equation* (5.3) *and the right hand side of equation* (5.4) *are Lipschitz continuous in the state and adjoint variables.*

Proof. This follows from their linearity in the state and adjoint variables. □

Theorem 5.3. *The solution to the optimality system is unique for a sufficiently small final time T*

Proof. Follows from lemmas 5.1 and 5.2, and theorem 2.3 in (Joshi et al., 2006). □

5.1.1 Interpretation of the optimal sampling policy

Theorem (5.2) characterizes the optimal sampling policy by introducing "adjoint variables," $\lambda_u(t)$ and $\lambda_o(t)$, the amount a manager would be willing to pay for a small decrease in the proportion of Undetected and Outbreak patches, at time t, respectively. To make sense of (5.6) note that $\lambda_u(t) - \lambda_d(t)$ is the cost benefit of eradicating a small proportion of Undetected patches and $U(t)/[1 - D(t) - O(t)]$ is the proportion of patches available for sampling that are infected. So equation (5.6) is just $1/2\epsilon$ times the per unit cost benefit of increasing sampling a small amount.

From the first equation in (5.4), the amount the manager is willing to pay decreases as the end of the management period approaches, and is highest in cases where the cost of damage in Undetected patches, k_u, and outbreak patches, k_o, is high. Naively, one might conclude from (5.6), that optimal sampling effort should increase with increased efficacy and decrease when sampling is costly or when there are many absent patches that must be sampled. However, this cannot be concluded directly from the equations due to how e_s, k_s, and $U(t)$ affect the adjoint equations in (5.4). Therefore, we must use numerical methods to analyze how most of the parameters affect optimal sampling effort.

5.1.2 Numerical methods

The solutions to the state and adjoint equations must be found numerically. To do so, we use the forward backward sweep method (Lenhart and Workman, 2007), which consists of the following steps:

1. Guess an initial sampling strategy, $s(t)$.
2. Solve the initial value problem, equation (5.2), forward in time, given this sampling strategy.
3. Solve the final value problem, equation (5.4), backwards in time, using $U(t)$, $D(t)$ and $O(t)$ generated from step (2).
4. Calculate the optimal sampling strategy, $s^*(t)$, using equation. (5.6), given $\lambda_u(t)$, $\lambda_d(t)$, $\lambda_o(t)$, $U(t)$, $D(t)$ and $O(t)$ calculated above.
5. Update the sampling strategy as $\hat{s}(t) = ps^*(t) + (1-p)s(t)$ with $0 < p \leq 1$.
6. Set $s(t) = \hat{s}(t)$ and repeat steps 2-5 until $s(t)$ and $\hat{s}(t)$ converge.

For many parameter combinations, especially for ϵ small, this method does not converge. In such cases, we used hill climbing instead of solving for $s^*(t)$ directly as in step (4). This can be achieved by replacing steps (4) and (5) with the update: $\hat{s} = s(t) - q\,\partial H/\partial s$, where $q = 0.005$. This method is slower, but converged for all parameter combinations tested. For several parameter combinations increasing q improves speed with no sacrifice to convergence.

5.1.3 Equilibrium and constant strategies

Optimal constant strategies were generated numerically using "`optimize`" in `R`, which uses a combination of golden section search and successive parabolic interpolation.

Equilibrium strategies were generated by solving for the optimal equilibrium that minimized long term cost. While equilibrium Undetected, Detected and Outbreak patch proportion, given sampling effort, s, can be calculated analytically, the equilibrium of the full seven dimensional system where the shadow prices, λ_u, λ_d and λ_o, are also at equilibrium is not tractable. Therefore, we solve for the equilibrium of equations (5.2) and (5.4) numerically using "`rootSolve`" in `R`, an implementation of the Newton-Raphson algorithm.

5.2 Appendix B: Parameterization for the eradication of Gypsy Moth

While our model does not explicitly consider patch size, we use the size of gypsy moth infestations on the west coast of the United States to estimate the parameters in our model. To do this we start with parameters defined in the literature and rescale them appropriately to match our continuous time formulation of sampling, eradication, and cost (see table 5.1).

Table 5.1: Known gypsy moth parameters from the literature that we rescaled to parameterize our model

Symbol	**Description**	**Value**	**Source**
τ	Average time it takes for an undetected patch to become an outbreak	13 years	eq. (5.9), using Epanchin-Niell et al. (2012)
τ_e	Average time it takes to eradicate an outbreak	4 years	Lane County Oregon eradication
a	Patch area	930 km^2	Lane County Oregon eradication
a_u	Mean treatment area of undetected infestations	6.1 km^2	Washington State Eradication Program
κ_d	Cost of damage by gypsy moth per year per km^2	380 USD	Sharov and Liebhold (1998)
κ_c	Cost of deploying pesticide per km^2	6965 USD	Mayo et al. (2003)
κ_s	Cost of deploying one trap per year	49.67 USD	Mayo et al. (2003)

Calculating sampling parameters: Consider a landscape of n patches, each patch with area a km^2. Let the size of an infestation in Undetected and Detected patches be denoted as a_u km^2 and let τ denote the average amount of time it takes for an Undetected or Detected patch to become an outbreak. Note that τ comes from how time is rescaled in the model. We assume that the probability that a single trap detects an infestation in one year equals the proportion of the total area of the patch that is occupied by the pest. This leads to

$$e_s = \frac{a_u \tau}{a}. \tag{5.8}$$

To estimate a, a_u and τ we use data from gypsy moth infestations on the west coast of the United States. The largest gypsy moth infestation ever successfully eradicated was a 930 km^2 region located in Lane County, Oregon. Therefore, we define a patch to be a region of area, $a = 930$ km^2, and assume the pest population in an Outbreak fully occupies the patch.

Since 1988 Washington state has eradicated several small isolated populations (agr.wa.gov/PlantsInsects/InsectPests/GypsyMoth). The mean treatment area of these infestations is 6.1 km^2. We assume this is the average size of a gypsy moth infestation in an Undetected patch, a_u.

To calculate τ, we use the model described by Epanchin-Niell et al. (2012). They described the total area cover (AC) of a t year old infestation in km^2 as

$$AC(t) = \pi \left(\sum_{i=1}^{t} \frac{1.5 i^5}{25 + i^5} \right)^2. \tag{5.9}$$

This model assumes radial spread with a sigmoidal density dependent spread rate,

to account for an Allee effect. Using equation (5.9) it takes 13 years to reach a size of 472 km^2, which is approximately the largest infestation in Washington state that was successfully eradicated in two treatments or less. Therefore, we let $\tau = 13$ years be the average time it takes for an Undetected patch to transition into an Outbreak. With a,a_u and τ described above, $e_s = 0.0857$ $traps^{-1}$. Note in unscaled time, e_s corresponds to a trapping efficacy of 0.0066 detections per trap per year.

We set the maximum sampling effort to be such that on average it takes two weeks to detect the presence of the invasive in an Undetected patch. Given there is 52.2 weeks in a year, we have

$$s_{max} = \frac{26.1\,\tau}{e_s} = 3960 \text{ traps} \tag{5.10}$$

Calculating eradication rates: Let τ_e be the average amount of time in years it takes to eradicate an Outbreak when treatment is being deployed continuously at a rate of one treatment per year. Then,

$$e_o = \frac{\tau}{\tau_e}. \tag{5.11}$$

Detected patches are eradicated at rate e_d, where non-immediate eradication is due to delays in deployment rather than failed eradication attempts. If τ_d the average amount of time in years it takes to eradicate a Detected patch then

$$e_d = \frac{\tau}{\tau_d}. \tag{5.12}$$

It took 4 years of pesticide treatments, from 1985 to 1988, to eradicate the Outbreak in Lane county Oregon and therefore we let $\tau_e = 4$ years, meaning $e_o = 3.25$. We vary τ_d in our study, but assume it is greater than 6 months and less than τ_e. As a baseline we set it equal to one year, giving $e_d = 13$.

Calculating cost parameters: Let κ_d be the cost of tree defoliation per km^2 of gypsy moth infestation per year, κ_c be the cost of deploying a single pesticide treatment per km^2 and κ_s be the cost of deploying and monitoring each trap per year. Then

$$\begin{aligned} k_u &= \kappa_d a_u \tau \\ k_o &= \kappa_d a \tau + \kappa_c a \tau \\ k_s &= \kappa_s \tau \\ k_d &= \kappa_d a_u \tau + e_d \kappa_c a_u. \end{aligned} \tag{5.13}$$

Damage due to defoliation is $\kappa_d = 380$ USD as estimated in (Sharov and Liebhold, 1998). The cost of deploying an eradication treatment is set to $\kappa_c = 6,965$ USD per km^2 as estimated in (Mayo et al., 2003). Trap cost is set at $\kappa_s = 49.67$ USD per trap per year, as estimated in (Mayo et al., 2003). This leads to parameters $k_u = 30.3$ thousand USD $\cdot$ patch^{-1}, $k_o = 88.8$ million USD $\cdot$ patch^{-1}, $k_d = 582.5$ thousand USD $\cdot$ patch^{-1}, and $k_s = 646$ USD $\cdot$ trap^{-1} $\cdot$ patch^{-1}.

In the above formulation, the cost of eradicating Outbreaks looks different than the cost of eradicating Detected patches. This is because delays in the eradication of Detected patches are assumed to be due to political or management delays and not failed eradication attempts. We assume there is no direct cost to waiting to eradicate a Detected patch. Therefore, the cost of eradicating Detected

patches is just the cost of applying treatment times the number of eradications. For an Outbreak patch, treatment costs accumulate from failed eradication attempts over the entire timespan prior to successful eradication.

We assume that $\epsilon = 0.01$ so that quadratic sampling cost is negligible compared to linear sampling costs for all trap densities.

Initial Conditions: Washington state is $184,827$ km^2, corresponding to approximately $n = 200$ patches in our model. During the first five years of their eradication program, starting in 1979, seven pesticide treatments were applied at four separate locations in King County, while smaller isolated treatments were applied in Clark, Pierce and Snohomish counties. Hence, we assumed an initial prevalence of one Outbreak patch and three Undetected patches, yielding initial conditions of $U(0) = 0.015$, and $O(0) = 0.005$.

5.3 Appendix C: Supplementary figures

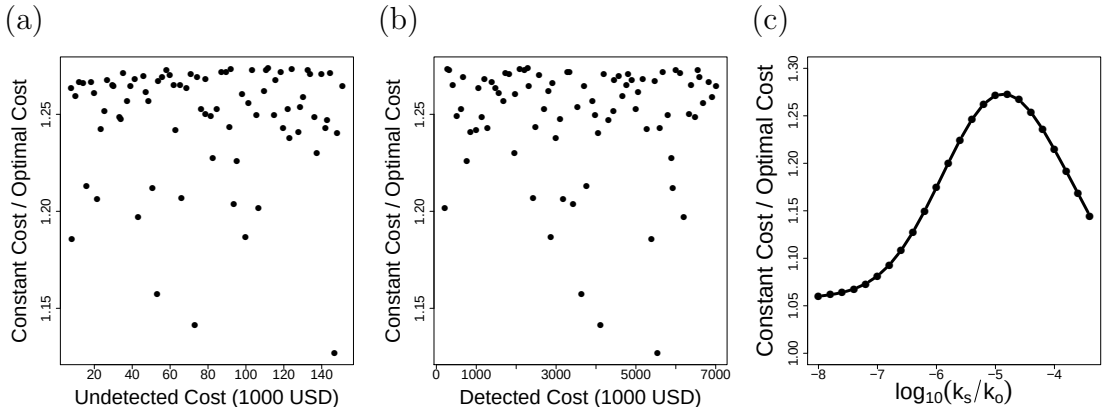

Figure 5.1: (a) How many times more costly it is to deploy the constant strategy over the intense early sampling strategy as a function of k_u, when varying k_s, k_o, k_d and k_u simultaneously using latin hypercube sampling. Note that k_u does not explain any of the variation in the relative cost benefit of using intense early sampling. (b) How many times more costly it is to deploy the constant strategy over the intense early sampling strategy as a function of k_d, when varying k_s, k_o, k_d and k_u simultaneously using latin hypercube sampling. Note that k_d does not explain any of the variation in the relative cost benefit of using intense early sampling. (c) How many times more costly it is to deploy the constant strategy over the intense early sampling strategy as a function of the base 10 logarithm of the ratio of sampling cost to Outbreak cost, i.e. how many orders of magnitude smaller k_s is than k_o. Other parameters are $\alpha = 0.0005, \gamma = 2, e_s = 0.087, e_o = 3.25, \epsilon = 0.01, \delta = 0.13, s_{max} = 3960$

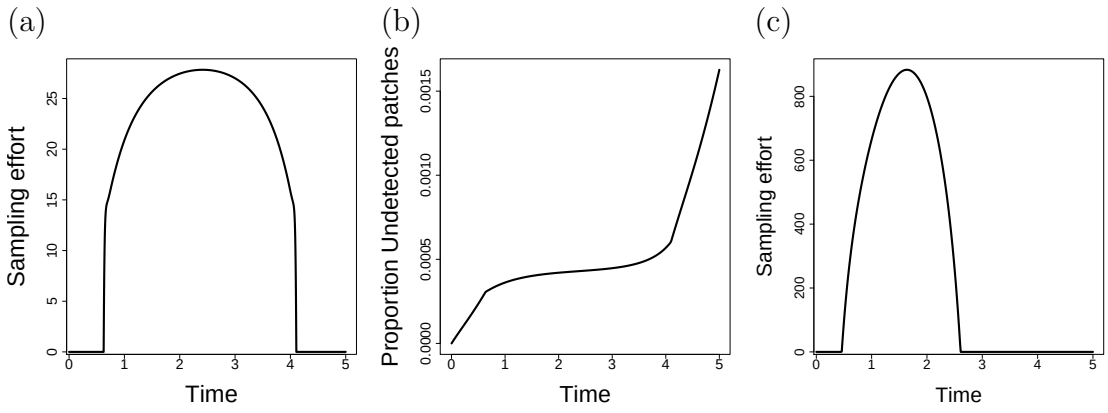

Figure 5.2: (a) Optimal per-patch sampling effort vs. time when the invader is initially absent. (b) The corresponding dynamics of the proportion of Undetected patches. (c) Optimal per-patch sampling effort vs. time when the invader is initially present but sampling efficacy is very low, $e_s = 0.002$.

CHAPTER 6

SUPPLEMENTARY INFORMATION FOR CHAPTER THREE

6.1 Validation of analytical results

To confirm that the escapement rules produced in the deterministic analysis is in fact producing the best constant escapement policy, we compared our analytic solutions to the best escapement strategies found via numerical optimization, when the initial conditions are set to the equilibrium biomass. When $\delta < \delta_{crit}$, the numeric solutions converged to a strategy of form $(\sigma = \sigma^*, \eta = 0)$ as in (3.22), when $\delta > \delta_{crit}$ and $a_{31}R(\sigma^*)/(1 - a_{11}) < (1 - a_{33})\sigma^*$, the numerics converged to a $(h = 0, s = s^*)$ strategy as in (3.35), and when $\delta > \delta_{crit}$ and $a_{31}R(\sigma^*)/(1-a_{11}) \geq (1-a_{33})\sigma^*$, they converged to $(\sigma = \hat{\sigma}^*, s = 0)$ as in (3.40) (figure 6.1). In these plots the discounted net revenue generated by our analytic solutions are compared to the revenue from the numerical optimal escapement strategy for 2000 parameter combinations, calculated using "optim", an implementation of the Nelder Mead simplex method in R (R Development Core Team, 2008), with stage structure transition parameters and discount rates generated uniform randomly with a Beverton-Holt recruitment function.

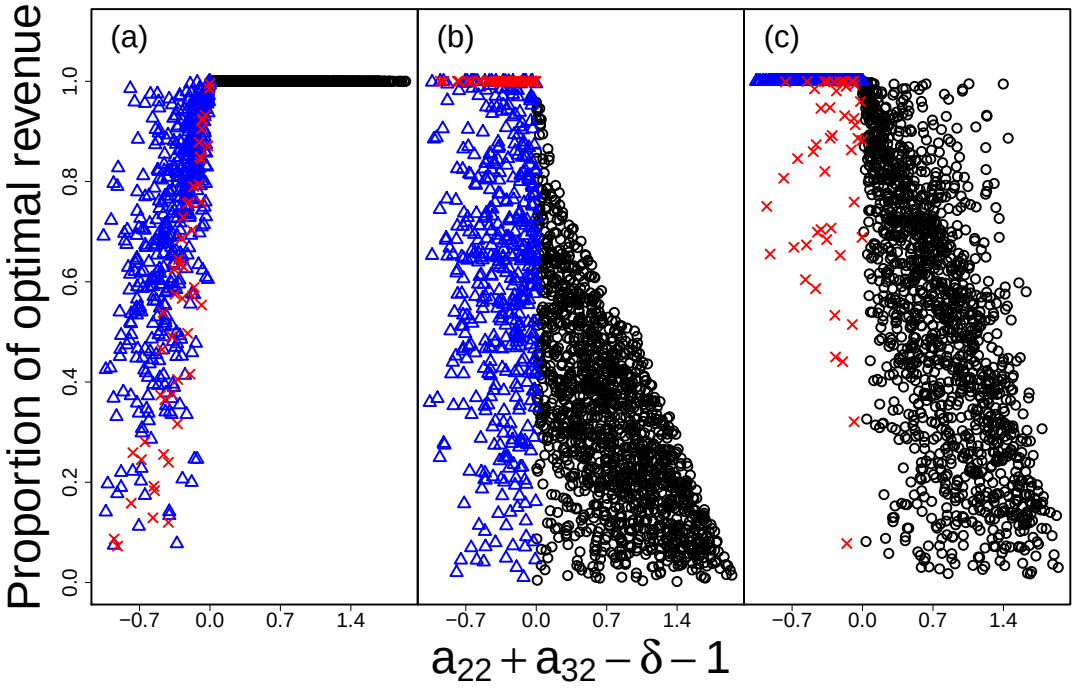

Figure 6.1: Plots of net revenue, relative to optimal net revenue, for a variety of harvesting strategies and conditions on the parameters. 2,000 parameter values were uniformly randomly generated over the domains $a_{32}, a_{21} \in (0,2)$, $a_{11}, a_{22}, a_{33} \in (0,1)$, $\delta \in (0, 0.1)$, throwing out any parameter combination not satisfying proposition 3.1. (a) Net revenue, relative to optimal net revenue, when harvesting no immatures and letting σ^* units of adult biomass escape. The numerical results here confirm the prediction that when $[a_{32} + a_{22} > 1 + \delta$; black circles] harvesting no immatures and letting σ^* adult biomass escape achieves the optimal revenue while not for other parameter combinations $[a_{32} + a_{22} < 1 + \delta$; red x's and blue triangles]. (b) Net revenue, relative to optimal net revenue, when harvesting no adults and letting s^* units of immature biomass escape, The numerical results here show that when $[a_{32} + a_{22} < 1 + \delta$ and $a_{31}R(\sigma^*)/(1 - a_{11}) < (1 - a_{33})\sigma^*$; red x's] this strategy is optimal. (c) net revenue, relative to optimal net revenue, when harvesting all immature fish and letting $\hat{\sigma}^*$ adults escape. This strategy is optimal when $[a_{32} + a_{22} < 1 + \delta$ and $a_{31}R(\sigma^*)/(1 - a_{11}) > (1 - a_{33})\sigma^*$; blue triangles]. Other parameters are $b_1 = 3.25$ and $b_2 = 0.00234$.

CHAPTER 7

SUPPLEMENTARY INFORMATION FOR CHAPTER FOUR

7.1 Survey

Below is a copy of the survey.

How many times have you played this game before?

- possible answers: "0","1", "2",... "15", "more than 15", "I've only played a different version of this game"

What best describes your education level?

- possible answers: "No college", "Some college or associates degree, but not currently in college", "Freshman (1st year)", "Sophomore (2nd year)", "Junior (3rd year)", "Senior (4th year or greater)", "completed Bachelor's degree", "In PhD, MS, MA, or MEng program", "In other post-bachelor program (e.g. JD, MBA, MD, MFA)", "completed MS, MA, or MEng degree", "completed PhD degree", "completed other post-bachelor degree (e.g. JD, MBA, MD, MFA)"

What best describes the field of study for your highest degree?

- possible answers: "No college", "Math, Statistics, or Computation"," Ecology, Natural Resources, or Environmental Biology", "Economics", "Political

Science or Government",“ Environmental Engineering", "Other Engineering", "Other Biology", "Physical Sciences", "Social Sciences", "Humanities, "undecided"

What best describes your experience fishing?

- possible answers: "I have never fished","I fish or have fished, but less than once per year", "I fish recreationally, at least once per year, but not for a living", "I fish or have fished for a living"

What best describes your experience managing fisheries?

- possible answers: "I have work/intern experience managing fisheries, more than 10 years", "I have work/intern experience managing fisheries, between 10 and 2 years", "I have work/intern experience managing fisheries, less than 2 years", " I am considering a career in fisheries management, but have no experience", " I am not considering a career in fisheries management"

Do you have work experience managing any (non-human) biological population outside of fisheries?

- possible answers: "I have work/intern experience managing game (hunted populations)", "I have work/intern experience in conservation biology", "I have work/intern experience in forestry", "I have work/intern experience in agricultural management", "I have work/intern experience managing other biological populations", "I am considering careers in managing biological populations, but have no experience", "I am not considering careers in managing biological populations"

7.2 Game directions

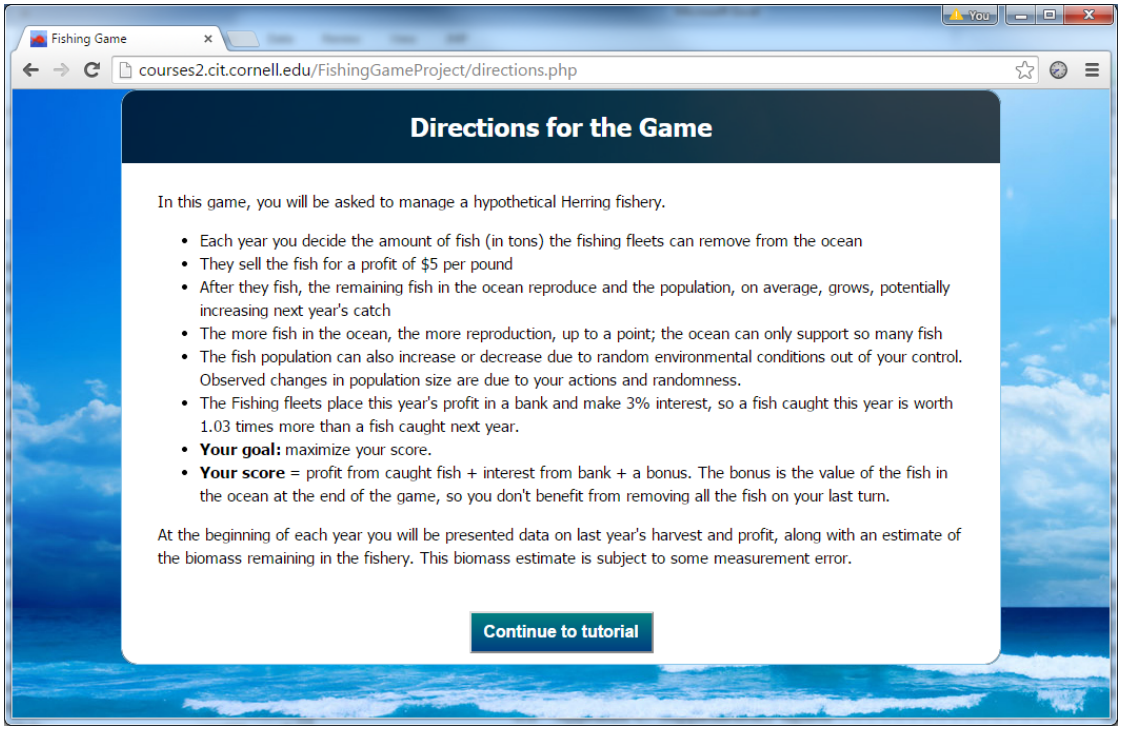

Figure 7.1: Directions for unstructured herring fish game.

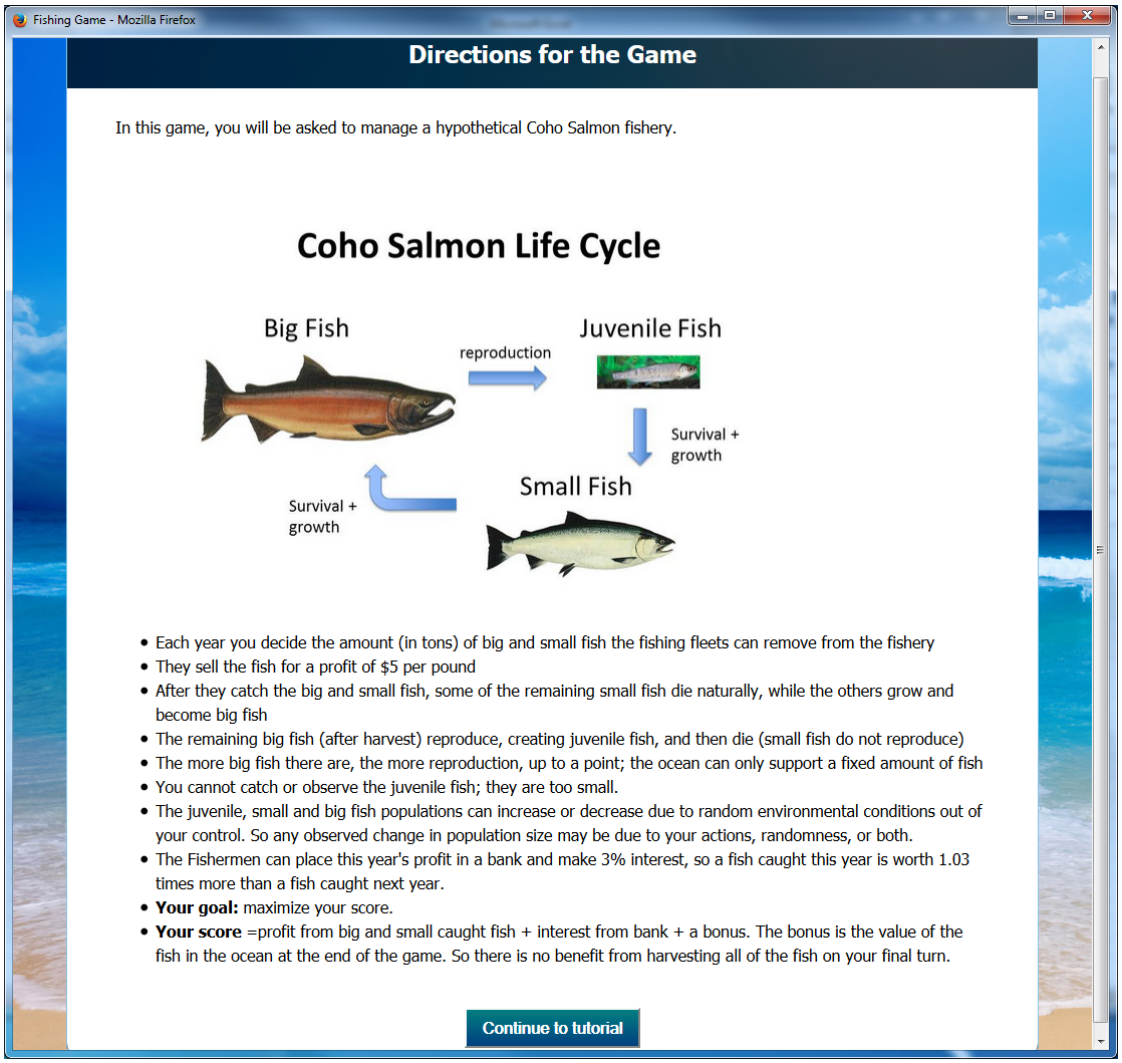

Figure 7.2: Directions for age structured salmon fish game.

7.3 Supplementary figures

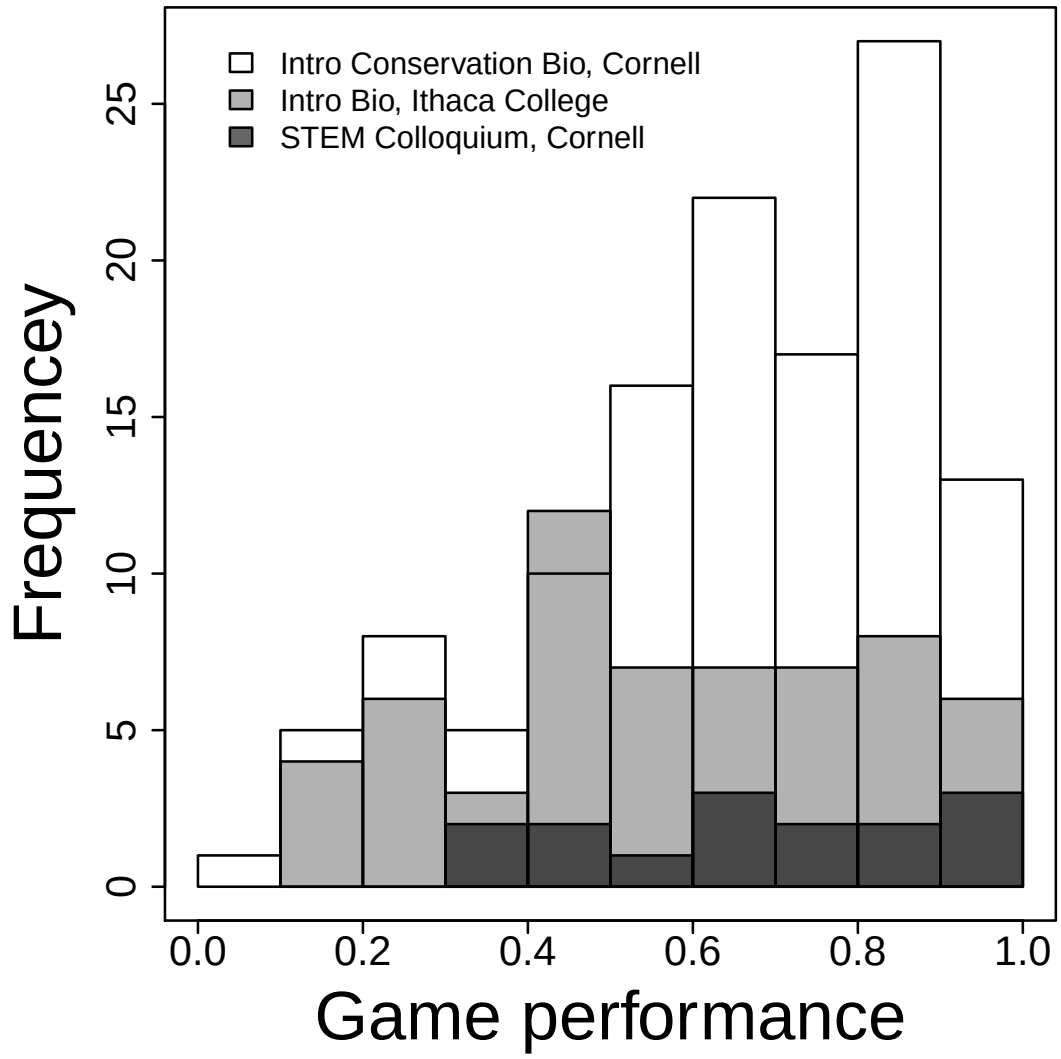

Figure 7.3: A histogram of percent of optimal profit achieved by the users for each class. Note the histograms are overlaid rather than stacked.

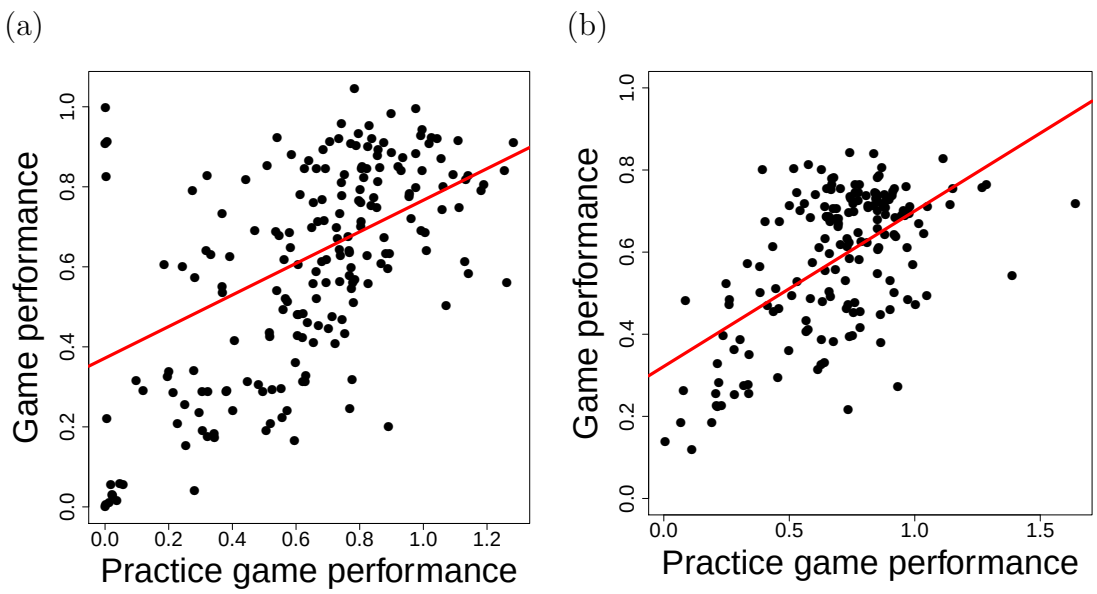

Figure 7.4: Proportion of optimal profit generated by the user in the actual game vs. Proportion of optimal profit generated by the user in the practice, not including the bonus, for (a) the one dimensional game and (b) the age structured game.

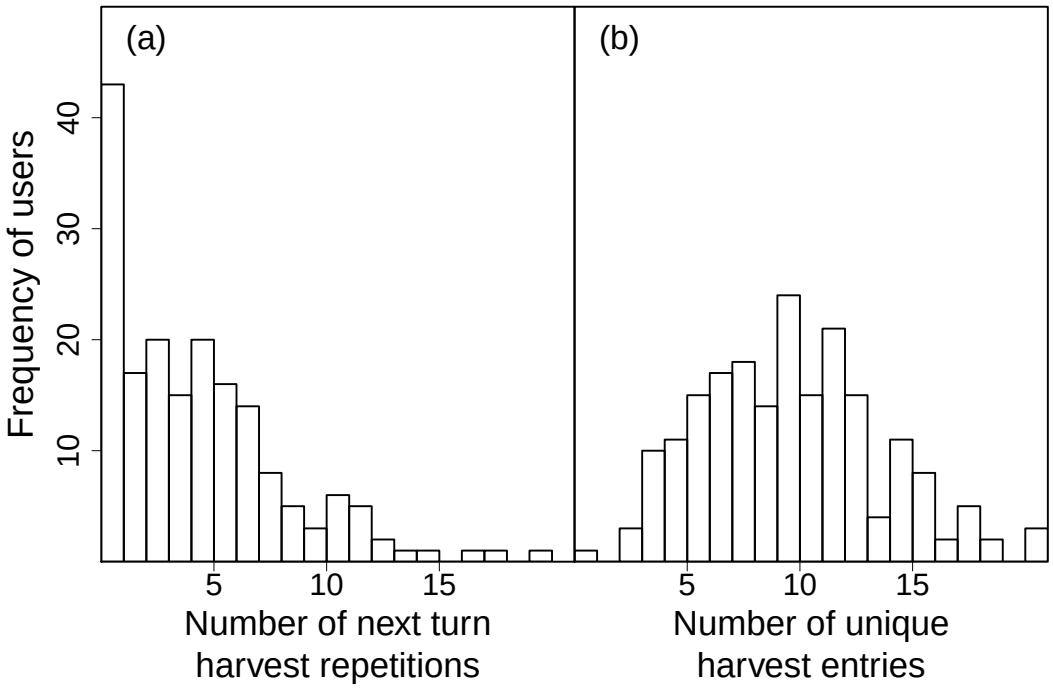

Figure 7.5: (a) A histogram of the number of times the user entered same harvest value as they did on the previous turn. (b) A histogram of the number of unique harvest entries they made over the course of the entire game.

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